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## ADVERTISEMENT.

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THE Committee appointed by the *Royal Society* to direct the publication of the *Philosophical Transactions* take this opportunity to acquaint the public that it fully appears, as well from the Council-books and Journals of the Society as from repeated declarations which have been made in several former *Transactions*, that the printing of them was always, from time to time, the single act of the respective Secretaries till the Forty-seventh Volume, the Society, as a Body, never interesting themselves any further in their publication than by occasionally recommending the revival of them to some of their Secretaries, when, from the particular circumstances of their affairs, the *Transactions* had happened for any length of time to be intermitted. And this seems principally to have been done with a view to satisfy the public that their usual meetings were then continued, for the improvement of knowledge and benefit of mankind the great ends of their first institution by the Royal Charters, and which they have ever since steadily pursued

But the Society being of late years greatly enlarged, and their communications more numerous, it was thought advisable that a Committee of their members should be appointed to reconsider the papers read before them, and select out of them such as they should judge most proper for publication in the future *Transactions*, which was accordingly done upon the 26th of March, 1752. And the grounds of their choice are, and will continue to be, the importance and singularity of the subjects, or the advantageous manner of treating them; without pretending to answer for the certainty of the facts, or propriety of the reasonings contained in the several papers so published, which must still rest on the credit or judgment of their respective authors.

It is likewise necessary on this occasion to remark, that it is an established rule of the Society, to which they will always adhere, never to give their opinion, as a Body,

upon any subject, either of Nature or Art, that comes before them. And therefore the thanks, which are frequently proposed from the Chair, to be given to the authors of such papers as are read at their accustomed meetings, or to the persons through whose hands they received them, are to be considered in no other light than as a matter of civility, in return for the respect shown to the Society by those communications. The like also is to be said with regard to the several projects, inventions, and curiosities of various kinds, which are often exhibited to the Society, the authors whereof, or those who exhibit them, frequently take the liberty to report, and even to certify in the public newspapers, that they have met with the highest applause and approbation. And therefore it is hoped that no regard will hereafter be paid to such reports and public notices, which in some instances have been too lightly credited, to the dishonour of the Society

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Institutions marked A are entitled to receive Philosophical Transactions, Series A, and Proceedings

"	"	B	"	"	"	"	Series B, and Proceedings
"	"	AB	"	"	"	"	Series A and B, and Proceedings
"	"	P	"	"	"	"	Proceedings only

## America (Central).

Mexico.

*p* Sociedad Científica "Antonio Alzate"

## America (North). (See UNITED STATES )

## America (South).

Buenos Ayres

*p* Museo de la Plata

AB Museo Nacional

Caracas.

B. University Library

Cordova.

AB Academia Nacional de Ciencias

Demerara.

*p* Royal Agricultural and Commercial Society, British Guiana

Rio de Janeiro

*p* Observatorio

## Australia.

Adelaide

*p*. Royal Society of South Australia

Brisbane

*p*. Royal Society of Queensland.

Melbourne.

*p* Observatory.

*p* Royal Society of Victoria.

AB. University Library

Sydney.

*p*. Geological Survey.

*p*. Linnean Society of New South Wales.

AB Royal Society of New South Wales.

AB University Library.

## Austria.

Agram.

*p*. Societas Historico-Naturalis Croatica

Brunn.

AB Naturforschender Verein

## Austria (continued)

Gratz

AB Naturwissenschaftlicher Verein für Steiermark

Heimannstadt

*p* Siebenburgischer Verein für die Naturwissenschaften

Innsbruck

AB Das Ferdinandeum

*p* Naturwissenschaftlich - Medicinischer Verein

Klausenburg

AB Az Erdélyi Múzeum Das Siebenburgische Museum

Prague

AB Königliche Böhmische Gesellschaft der Wissenschaften

Schemnitz

*p* K Ungarische Berg- und Forst-Akademie

Trieste

B Museo di Storia Naturale

*p*. Società Adriatica di Scienze Naturali

Vienna

*p* Anthropologische Gesellschaft

AB Kaiserliche Akademie der Wissenschaften

*p* K K Geographische Gesellschaft

AB K K Geologische Reichsanstalt

B K K Zoologisch-Botanische Gesellschaft

B. Naturhistorisches Hof-Museum

*p* Oesterreichische Gesellschaft für Meteorologie

## Belgium.

Brussels.

B. Académie Royale de Médecine

AB. Académie Royale des Sciences

B. Musée Royal d'Histoire Naturelle de Belgique

*p*. Observatoire Royal

*p* Société Malacologique de Belgique

## Belgium (continued)

### Ghent

AB University

### Liège.

AB Société des Sciences

p Société Géologique de Belgique.

### Louvain

p Laboratoire de Microscopie et de Biologie  
Cellulaire

AB. L'Université

## Canada.

### Hamilton

p Hamilton Association

### Montreal.

AB McGill University.

p Natural History Society

### Ottawa

AB Geological Survey of Canada

AB Royal Society of Canada

### Toronto.

p Astronomical and Physical Society.

p Canadian Institute

AB University

## Cape of Good Hope.

A. Observatory

AB South African Library

## Ceylon.

### Colombo

B. Museum

## China.

### Shanghai

p China Branch of the Royal Asiatic Society

## Denmark.

### Copenhagen.

AB Kongelige Danske Videnskabernes Selskab

## England and Wales.

### Aberystwith

AB. University College

### Bangor

AB. University College of North Wales

### Birmingham

AB Free Central Library.

AB. Mason College

p. Philosophical Society.

### Bolton.

p. Public Library.

### Bristol.

p. Merchant Venturers' School.

### Cambridge

AB Philosophical Society.

p. Union Society.

### Cooper's Hill.

AB. Royal Indian Engineering College

## England and Wales (continued)

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p Dudley and Midland Geological and  
Scientific Society

### Essex

p Essex Field Club

### Greenwich

A Royal Observatory

### Kew

B Royal Gardens

### Leeds

p Philosophical Society

AB Yorkshire College

### Liverpool

AB Free Public Library.

p. Literary and Philosophical Society

A Observatory

AB University College

### London.

AB Admiralty

p Anthropological Institute

B British Museum (Nat Hist)

AB Chemical Society

p "Electrician," Editor of the

B Entomological Society

AB Geological Society

AB Geological Survey of Great Britain

p Geologists' Association

AB Guildhall Library

A Institution of Civil Engineers.

A. Institution of Mechanical Engineers

A Institution of Naval Architects

p Iron and Steel Institute

AB. King's College

B Linnean Society.

AB. London Institution

p. London Library.

A Mathematical Society

p. Meteorological Office

p Odontological Society.

p Pharmaceutical Society.

p. Physical Society

p Quekett Microscopical Club.

p. Royal Agricultural Society

p Royal Asiatic Society

A. Royal Astronomical Society

B Royal College of Physicians.

B. Royal College of Surgeons.

p. Royal Engineers (for Libraries abroad, six  
copies).

AB Royal Engineers. Head Quarters Library.

p. Royal Geographical Society.

p. Royal Horticultural Society

p Royal Institute of British Architects.

**England and Wales (continued)****London (continued)**

- AB Royal Institution of Great Britain
- B Royal Medical and Chirurgical Society
- p Royal Meteorological Society
- p Royal Microscopical Society
- p Royal Statistical Society
- AB Royal United Service Institution
- AB Society of Arts
- p Society of Biblical Archaeology
- p Society of Chemical Industry (London Section)
- p Standard Weights and Measures Department
- AB The Queen's Library
- AB The War Office
- AB University College
- p Victoria Institute.
- B Zoological Society

**Manchester**

- AB Free Library
- AB Literary and Philosophical Society
- p Geological Society
- AB Owens College.

**Notley**

- p Royal Victoria Hospital

**Newcastle**

- Free Library
- p North of England Institute of Mining and Mechanical Engineers
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**Norwich**

- p Norfolk and Norwich Literary Institution

**Oxford**

- p Ashmolean Society
- AB Radcliffe Library
- A Radcliffe Observatory

**Penzance**

- p Geological Society of Cornwall

**Plymouth**

- B. Marine Biological Association
- p Plymouth Institution

**Richmond**

"Kew" Observatory

**Salford**

- p Royal Museum and Library

**Stonyhurst**

- p The College

**Swansea**

- AB Royal Institution

**Woolwich**

- AB. Royal Artillery Library

**Finland.****Helsingfors**

- p Societas pro Fauna et Flora Fennica
- AB Société des Sciences

**France****Bordeaux**

- p Académie des Sciences
- p Faculté des Sciences
- p Société de Médecine et de Chirurgie
- p Société des Sciences Physiques et Naturelles

**Cherbourg**

- p Société des Sciences Naturelles

**Dijon**

- p Académie des Sciences

**Lille**

- p Faculté des Sciences

**Lyons**

- AB Académie des Sciences, Belles-Lettres et Arts

**Marseille**

- p Faculté des Sciences

**Montpellier**

- AB Académie des Sciences et Lettres
- B Faculté de Médecine

**Paris**

- AB Académie des Sciences de l'Institut
- p Association Française pour l'Avancement des Sciences
- p Bureau des Longitudes
- p Bureau International des Poids et Mesures
- p Commission des Annales des Ponts et Chaussées
- p Conservatoire des Arts et Métiers
- p Cosmos (M. L'ABBÉ VALETTE)
- AB Dépôt de la Marine
- AB École des Mines
- AB École Normale Supérieure
- AB École Polytechnique
- AB Faculté des Sciences de la Sorbonne
- AB Jardin des Plantes
- A L'Observatoire
- p Revue Internationale de l'Électricité
- p Revue Scientifique (Mons H. DE VARIGNY)
- p. Société de Biologie
- AB Société d'Encouragement pour l'Industrie Nationale
- AB Société de Géographie
- p Société de Physique
- B Société Entomologique
- AB Société Géologique.
- p Société Mathématique
- p Société Météorologique de France

**Toulouse**

- AB Académie des Sciences
- A. Faculté des Sciences



**Germany.**

**Berlin**

- A Deutsche Chemische Gesellschaft
- A Die Steinwarte
- p Gesellschaft für Erdkunde
- AB Königliche Preussische Akademie der Wissenschaften
- A Physikalische Gesellschaft

**Bonn**

- AB Universität

**Bremen**

- p Naturwissenschaftlicher Verein

**Breslau**

- p Schlesische Gesellschaft für Vaterländische Kultur

**Brunswick**

- p Verein für Naturwissenschaft-

**Carlsruhe See Karlsruhe**

**Danzig**

- AB Naturforschende Gesellschaft

**Dresden**

- p Verein für Erdkunde

**Emden**

- p Naturforschende Gesellschaft

**Erlangen.**

- AB. Physikalisch-Medicinische Societat

**Frankfurt-am-Main**

- AB Senckenbergische Naturforschende Gesellschaft
- p Zoologische Gesellschaft.

**Frankfurt-am-Oder**

- p Naturwissenschaftlicher Verein

**Freiburg-im-Breisgau**

- AB Universität

**Giessen**

- AB Grossherzogliche Universität

**Gorlitz**

- p. Naturforschende Gesellschaft

**Göttingen**

- AB Königliche Gesellschaft der Wissenschaften

**Halle**

- AB Kaiserliche Leopoldino - Carolinische Deutsche Akademie der Naturforscher
- p. Naturwissenschaftlicher Verein für Sachsen und Thüringen

**Hamburg**

- p Naturhistorisches Museum.
- AB. Naturwissenschaftlicher Verein

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- p Naturhistorisch-Medicinische Gesellschaft
- AB. Universität.

**Germany (continued)**

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- AB Medicinisch-Naturwissenschaftliche Gesellschaft

**Karlsruhe**

- A Grossherzogliche Steinwarte

**Kiel**

- A Sternwarte
- AB Universität

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- AB Königliche Physikalisch - Ökonomische Gesellschaft

**Leipzig**

- p Annalen der Physik und Chemie
- A Astronomische Gesellschaft
- AB Königliche Sachsische Gesellschaft der Wissenschaften

**Magdeburg**

- p Naturwissenschaftlicher Verein

**Marburg**

- AB Universität.

**Munich**

- AB Königliche Bayerische Akademie der Wissenschaften
- p Zeitschrift für Biologie

**Münster**

- AB Königliche Theologische und Philosophische Akademie

**Potsdam**

- A. Astrophysikalisches Observatorium

**Rostock**

- AB Universität

**Strasbourg**

- AB Universität

**Tübingen.**

- AB Universität

**Würzburg**

- AB Physikalisch-Medicinische Gesellschaft

**Holland. (See NETHERLANDS)**

**Hungary.**

**Pesth**

- p Königl Ungarische Geologische Anstalt
- AB Á Magyar Tudós Társaság Die Ungarische Akademie der Wissenschaften

**India.**

**Bombay**

- AB Elphinstone College

**Calcutta**

- AB Asiatic Society of Bengal
- AB Geological Museum
- p Great Trigonometrical Survey of India
- AB. Indian Museum
- p The Meteorological Reporter to the Government of India.

**India (continued)****Madras**

- B Central Museum
- A Observatory.

**Roorkee**

- p Roorkee College

**Ireland****Armagh**

- A Observatory

**Belfast**

- AB Queen's College

**Cork**

- p Philosophical Society
- AB Queen's College

**Dublin**

- A Observatory
- AB National Library of Ireland
- B Royal College of Surgeons in Ireland
- AB Royal Dublin Society
- AB Royal Irish Academy

**Galway**

- AB Queen's College

**Italy****Bologna**

- AB Accademia delle Scienze dell' Istituto

**Florence**

- p Biblioteca Nazionale Centrale
- AB Museo Botanico
- p Reale Istituto di Studi Superiori

**Genoa**

- p Società Linguistica di Scienze Naturali e Geografiche

**Milan**

- AB Reale Istituto Lombardo di Scienze, Lettere ed Arti
- AB Società Italiana di Scienze Naturali

**Naples**

- p Società di Naturalisti
- AB Società Reale, Accademia delle Scienze
- B Stazione Zoologica (Dr DOHRN)

**Padua**

- p University

**Pisa**

- p Società Toscana di Scienze Naturali.

**Rome**

- p Accademia Pontificia de' Nuovi Lincei
- A. Reale Ufficio Centrale di Meteorologia e di Geodinamica, Collegio Romano
- AB. Reale Accademia dei Lincei.
- p R Comitato Geologico d' Italia
- AB Società Italiana delle Scienze

**Siena**

- p. Reale Accademia dei Fisiocritici

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**Italy (continued)****Turin**

- p Laboratorio di Fisiologia
- AB Reale Accademia delle Scienze

**Venice**

- p Ateneo Veneto
- AB. Reale Istituto Veneto di Scienze, Lettere ed Arti

**Japan.****Tokiô**

- AB Imperial University

**Yokohama**

- p Asiatic Society of Japan

**Java****Batavia**

- AB Bataviaasch Genootschap van Kunsten en Wetenschappen

**Buitenzorg**

- p Jardin Botanique

**Luxembourg.****Luxembourg**

- p Société des Sciences Naturelles

**Malta**

- p Public Library

**Mauritius**

- p Royal Society of Arts and Sciences

**Netherlands****Amsterdam**

- AB Koninklijke Akademie van Wetenschappen.
- p K Zoologisch Genootschap 'Natura Artis Magistra'

**Delft**

- p École Polytechnique

**Haarlem**

- AB Hollandsche Maatschappij der Wetenschappen
- p Musée Teyler

**Leyden**

- AB University

**Rotterdam**

- AB Bataafsch Genootschap der Proefondervindelijke Wijsbegeerte

**Utrecht.**

- AB Provinciaal Genootschap van Kunsten en Wetenschappen

**New Zealand****Wellington**

- AB New Zealand Institute

**Norway.****Bergen**

- AB Bergenske Museum

**Christiana**

- AB Kongelige Norske Frederiks Universitet

**Norway (continued)**

Tromsøe

*p* Museum

Trondhjem

AB Kongelige Norske Videnskabers Selskab

**Nova Scotia.**

Halifax

*p* Nova Scotian Institute of Science

Windsor

*p* King's College Library**Portugal**

Coimbra

AB Universidade

Lisbon

AB Academia Real das Sciencias

*p* Secção dos Trabalhos Geologicos de Portugal**Russia**

Dorpat

AB Université

Kazan

AB Imperatorsky Kazansky Universitet

Kharkoff

*p* Section Médicale de la Société des Sciences  
Expérimentales, Université de Kharkow

Kieff

*p* Société des Naturalistes

Moscow

AB Le Musée Public

B Société Impériale des Naturalistes

Odessa

*p* Société des Naturalistes de la Nouvelle-  
Russie

Pulkowa

A Nikolai Haupt-Sternwarte

St Petersburg

AB Académie Impériale des Sciences

AB Comité Géologique.

*p* Compass Observatory

A L'Observatoire Physique Central

**Scotland.**

Aberdeen

AB University

Edinburgh

*p* Geological Society.*p* Royal College of Physicians (Research  
Laboratory)*p* Royal Medical Society

A Royal Observatory

*p* Royal Physical Society*p* Royal Scottish Society of Arts.

AB Royal Society

Glasgow

AB Mitchell Free Library

*p* Philosophical Society**Servia**

Belgrade

*p* Académie Royale de Serbie.**Sicily**

Acireale

*p* Società Italiana dei Microscopisti

Catania

AB Accademia Gioenia di Scienze Naturali

Palermo

A Circolo Matematico.

AB. Consiglio di Perfezionamento (Società di  
Scienze Naturali ed Economiche)

A Reale Osservatorio

**Spain.**

Cadiz

A Observatorio de San Fernando

Madrid

*p* Comisión del Mapa Geológico de España

AB Real Academia de Ciencias

**Sweden.**

Gottenburg

AB Kongl Vetenskaps och Vitterhets Sam-  
halle

Lund

AB Universitet

Stockholm

A Acta Mathematica

AB Kongliga Svenska Vetenskaps-Akademie

AB Sveriges Geologiska Undersökning.

Upsala

AB Universitet

**Switzerland**

Basel

*p* Naturforschende Gesellschaft

Bern

AB Allg Schweizerische Gesellschaft.

*p* Naturforschende Gesellschaft

Geneva

AB Société de Physique et d'Histoire Naturelle.

AB Institut National Genevois

Lausanne

*p* Société Vaudoise des Sciences Naturelles.

Neuchâtel

*p* Astronomische Mittheilungen (Professor R.  
WOLF)*p* Société des Sciences Naturelles

Zurich

AB Das Schweizerische Polytechnikum

*p* Naturforschende Gesellschaft.**Tasmania.**

Hobart

*p* Royal Society of Tasmania.

**United States.**

Albany

AB New York State Library

Annapolis.

AB Naval Academy

Baltimore

AB Johns Hopkins University

Berkeley

p University of California

Boston

AB American Academy of Sciences

B Boston Society of Natural History

A Technological Institute

Brooklyn

AB Brooklyn Library

Cambridge

AB. Harvard University

B. Museum of Comparative Zoology

Chapel Hill (N C )

p Elisha Mitchell Scientific Society

Charleston

p. Elliott Society of Science and Art of South Carolina

Chicago.

AB. Academy of Sciences

Cincinnati

p Journal of Comparative Neurology.

Davenport (Iowa).

p. Academy of Natural Sciences

Madison.

p. Wisconsin Academy of Sciences

Mount Hamilton (California)

A Lick Observatory

New Haven (Conn ).

AB American Journal of Science

AB. Connecticut Academy of Arts and Sciences

**United States (continued)**

New York

p American Geographical Society

p American Museum of Natural History

p New York Academy of Sciences

p New York Medical Journal

p School of Mines, Columbia College

Philadelphia

AB Academy of Natural Sciences

AB American Philosophical Society

p Franklin Institute

p Wagner Free Institute of Science

Rochester (N Y )

p Academy of Science

St Louis

p Academy of Science

Salem (Mass )

p American Association for the Advancement of Science

p Essex Institute.

AB Peabody Academy of Science

San Francisco

AB California Academy of Sciences

Washington

p Department of Agriculture

A Office of the Chief Signal Officer

AB Patent Office

AB Smithsonian Institution

AB United States Coast Survey

p United States Commission of Fish and Fisheries

AB United States Geological Survey

AB United States Naval Observatory

West Point (N Y )

AB United States Military Academy



ADJUDICATION of the MEDALS of the ROYAL SOCIETY for the year 1891,  
by the PRESIDENT and COUNCIL.

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The COPLEY MEDAL to STANISLAO CANNIZZARO, For Mem.R S , for his Contributions to Chemical Philosophy, especially for his Application of AVOGADRO's Theory.

A ROYAL MEDAL to CHARLES LAPWORTH, F R S , for his Researches among the Older Rocks of Britain.

A ROYAL MEDAL to ARTHUR WILLIAM RUCKER, F R.S , for his Researches on Liquid Films, and his Contributions to our Knowledge of Terrestrial Magnetism.

The DAVY MEDAL to VICTOR MEYER, for his Researches on the Determination of Vapour Densities at High Temperatures.

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The Bakerian Lecture, "On Tidal Prediction," was delivered by Professor G H DARWIN, F.R.S.

The Croonian Lecture, "On the Mammalian Nervous System, its Functions, and their Localisation determined by an Electrical Method," was delivered by FRANCIS GOTCH, and Professor VICTOR HORSLEY, F.R.S.



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# PHILOSOPHICAL TRANSACTIONS.

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I *The Patterns in Thumb and Finger Marks.*—On their arrangement into naturally distinct classes, the permanence of the papillary ridges that make them, and the resemblance of their classes to ordinary genera.

By FRANCIS GALTON, F.R.S.

Received November 3,—Read November 27, 1890

[PLATES 1, 2]

I PROPOSE to describe some results of a recent inquiry into the patterns formed by the papillary ridges upon the bulbs of the thumbs and fingers of different persons. The points upon which I shall chiefly dwell are, the classification of the patterns, their permanence throughout life, and the apt confirmation they afford of certain views concerning the more important conditions by which the genera of plants and animals are determined

My attention was drawn to the subject nearly three years ago, when preparing a lecture for the Royal Institution on "Personal Identification." (See either the 'Journal of the Royal Institution,' for Friday, May 25th, 1888, or 'Nature,' June 28th, 1888, in which the portion of the lecture with which we are now concerned is printed)

I would refer to that lecture, as it contains numerous references to the existing literature on the subject, and because it formed the starting point from which the present inquiry proceeded. Two conclusions were strongly impressed on my mind at the time when I gave it —

(1) That although much had been asserted as to the permanence of these markings, and though I was then able, through the kindness of Sir W. J. HERSCHEL, to submit two instances in proof, the truth of the assertion had never been adequately investigated.

(2) That the method of classifying the markings, which was originated by PURKINJE, in his 'Commentatio,' dated 1823 (a copy of this rare pamphlet is now

in the library of the College of Surgeons), and subsequently adopted by other writers, with more or less variation, was not based on a sufficiently good foundation.

Since then I have steadily pursued the inquiry and found its interests to widen considerably as I proceeded. They led in many directions, and among others to the topic that will be the last discussed.

### *Data*

The data on which this memoir is based are —

(1) The impressions of the two thumbs of about 2500 persons made for me, at my Anthropometric Laboratory, together with several impressions of the fingers.

(2) A small and unique collection of impressions put at my disposal by Sir W J HERSCHEL, of which one half were taken many years ago, and the other half were taken quite recently from the same persons. I will speak of these more at length when the time comes for using them.

As regards the first set —

I chose the two thumbs rather than two adjacent fingers on the same hand, in order to obtain data respecting symmetry, on which however very little will be said here, and I chose a thumb of each hand, rather than a finger of each hand, because the thumb being greater than that of the finger the width of it affords a proportionately larger field for variety of pattern. However, all that will be said about thumb marks, applies with but little reservation to finger marks, but with much more reservation to those of the toe.

I have myself not studied the latter, but PURKINJE states that the patterns of the toes are always of that particular sort which I shall define later on, and call a loop.

### *Origin of the Ridges*

I do not attempt to discuss the origin of the papillary ridges, because my knowledge is entirely second hand, and it would be presumptuous in me to do so. It will be sufficient to say that KOLLMANN'S (A. KOLLMANN, 'Der Tastapparat der Hand' Hamburg and Leipzig, LEOPOLD VOSS, 1883) dissections seem to prove (see his figs 19, 20) —

(1) That each of the papillæ (which lie below the cuticle) has two heads, which I will symbolise by the fork in the printed capital letter Y.

(2.) That the duct of the sudorific glands in passing outwards between the papillæ, is bound up, as in a bundle, with the adjacent head of each of two neighbouring papillæ. So that if the sudorific duct is symbolised by the printed letter I, a section across the ridges might be symbolised by a row of the letters Y and I printed alternately, thus—YIYIYIY. Then the union of the I with the adjacent prongs of two Y's forms the foundation of a ridge, and the clefts between the heads of the Y's correspond to the furrows.

There is, I believe, no adequate explanation of the fact that the prominences through which the ducts issue, on the bulbs of the finger, and in some other parts, are strongly disposed to arrange themselves into continuous ridges, and not to form isolated craters. There is, however, abundant analogy in the animal kingdom of external ridges of various sorts running in a variety of spirals and whorls.

### *Obtaining Impressions*

The impressions in my collection were made by thinly inking a copper plate with printer's ink, by means of a printer's roller. The plate was about eight inches by twelve, and fixed to a solid block of wood. The thumb was rather lightly rolled on the inked plate, not simply pressed upon it, and then rolled on paper. Thus the impression it left was a cylindrical projection of the whole bulb of the thumb, extending nearly from one side round to the other (fig. 8), and including all the principal characteristics of the pattern, which a simple impression (see those in Plate 2) often does not. The thumbs were easily cleaned by dipping them into a dish of turpentine and wiping with a cloth. It is an essential condition for making clear impressions that the ink should not lie low down the sides of the ridges. The furrows should remain quite uninked. I had much difficulty at first in contriving a rough and ready method of obtaining good impressions, and do not say that the plan just described is the best. But it has acted well for a long time, and, therefore, it is hardly necessary for me to speak here of later experiments to improve it.

### *Reversal of Patterns.*

Patterns of similar kinds lie on the two thumbs in opposite directions. They should never be read from right to left, but from outwards, inwards. Consequently, in order to make the pattern on the one thumb comparable with that on the other, it must be reversed. It is convenient to take a duplicate of the impressions upon tracing cloth, which shows the reversed pattern when it is viewed face downwards.

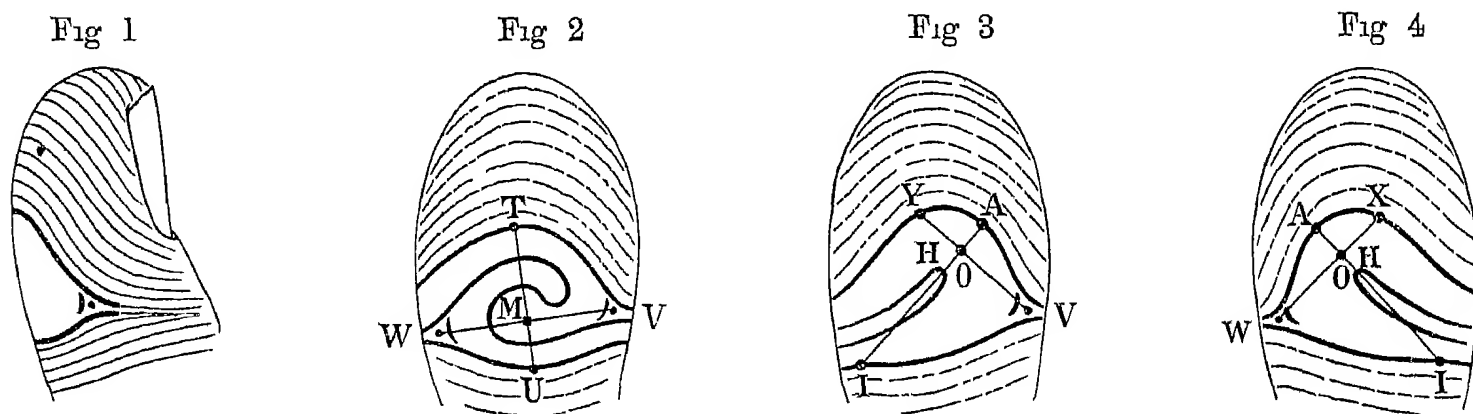
### *Origin of the Patterns.*

The reason why the patterns appear on the bulbs of the thumb and finger is apparently to be found in the presence of the thumb nail, which disarranges the otherwise parallel course of the ridges in the way that is diagrammatically shown in fig. 1.

Here we see that the upper ridges near the tip of the thumb are thrown into bold arches, while the ridges that lie below the level of the nail run horizontally. There is, in consequence, a tendency to leave an interspace, which has somehow to be filled up with a scroll work of ridges, and this scroll work constitutes the patterns with which we are concerned.

In about one case in thirty, the interspace is avoided by an arrangement like that in  $\alpha$ , figs. 7 and 9, but this is an unstable form, or it often shows signs of having

been on the point of breaking into a different pattern, as will soon be explained more fully. I call these patterns "Primaries," because they are the fundamental arrangement from which all the vast varieties of other patterns are lineally descended, and in all of which the interspace of which we have spoken exists.



### *Points of Reference*

Wherever an interspace occurs, two ridges must have diverged in order to make room for it. There may be a divergence of the ridges on both sides of the interspace, as in fig 2, or on one side only, as in figs. 3 and 4. Moreover, just in front of the place in the furrow, beyond which the parallel ridges begin to diverge, there are always one or more little cross lines, diagrammatically shown in all these figures, which cut off a small triangle.

The centres of these triangles form excellent spots or points of reference, though doubt may exist as to the exact position in which they should be placed. It is easy enough to determine their position approximately, and that is all we want.

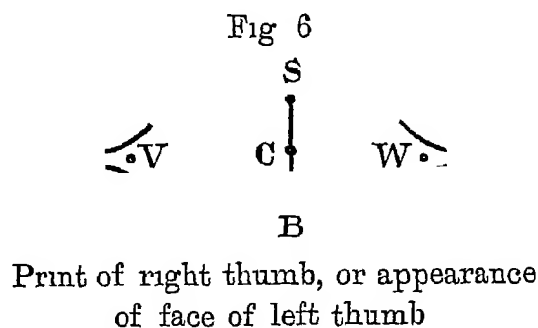
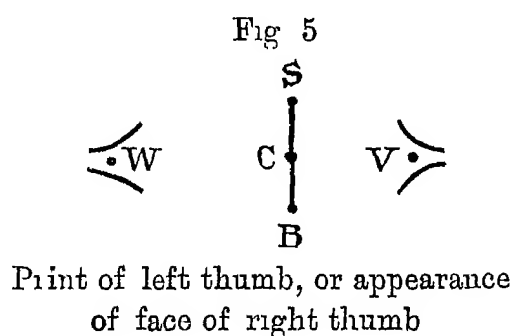
Hereafter I shall always call these two points V and W. V being to the outside of the thumb, and W to the inside, that is to say, nearest to the rest of the hand. They are cardinal points in my classification, and are very useful in constituting the two ends of a base line (fig 2) from which measurements may be made and bearings taken.

### *Reversals*

After the proper letters have been affixed to the points, it does not matter whether the pattern we are studying is direct or reversed. There is a curious variety in the way in which patterns are apt to be presented. Those on the right thumb are reversed forms of those met with on the left. The impression is the reversed form of the pattern itself. If made on a lithographic stone, it is re-reversed in the print. If made on transfer paper and thence put on the stone, it is re-re-reversed in the print. This is enough to show the confusion that will arise if the points V and W are not lettered, but it by no means exhausts the list of ordinary contingencies. As the letters V and W are unchanged in shape when they are reversed, they are convenient for the purpose to which they are here applied.

*Basis of the Classification*

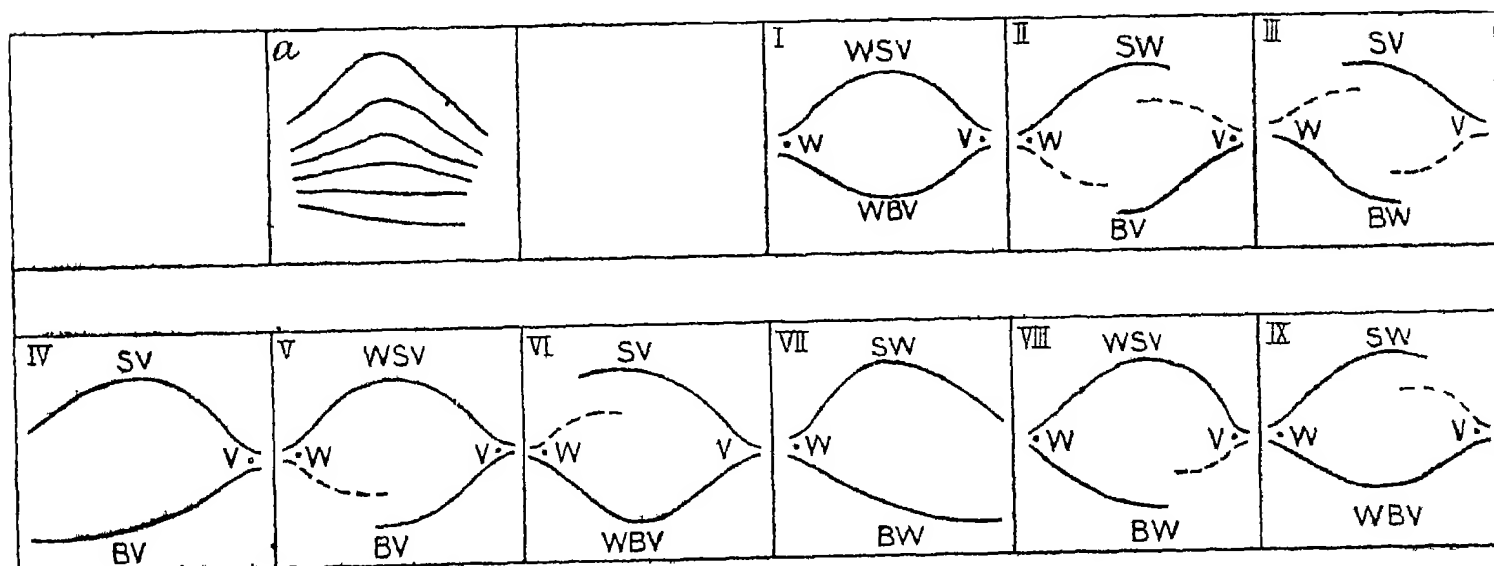
In one respect the divergent lines that bound the pattern admit, in the earlier part of their courses, of nine, and only nine, possible variations. Draw a line (figs. 5, 6) through what appears to be the most central part of the pattern (which we may call C), that shall be roughly parallel to the median line of the thumb, and shall cut



the upper boundary of the pattern at S and the lower boundary at B. Consequently, S and B, whose positions are very roughly determined, may be taken to represent the summit and the base of the pattern. Now the ridge in which S is situated must, by construction, have come either from V or from W, or from both. There are these three, and only these three, alternatives, SV, SW, WSV. Similarly, as regards the ridge on which B is situated, there are the three alternatives, BV, BW, WBV. As any one of the former events may be combined with any one of the latter, there are  $3 \times 3$ , or nine possible combinations. In the primaries neither V nor W exist, so they form a class by themselves, making a total of ten classes. The nine of which we have been speaking are as follows.—

I. WSV—WBV	IV. SV—BV	VII. SW—BW
II. SW—BV	V. WSV—BV	VIII. WSV—BW
III. SV—BW	VI. SV—WBV	IX. SW—WBV

Fig 7



These, as well as the primary, which is distinguished by the letter  $\alpha$ , are drawn in the diagram, fig 7.



*Outlines of the Patterns*

A pattern is quickly analysed by following with a pencil the course of the two pair of divergent ridges from V and W respectively (fig 8), or if one of these points

Fig 8

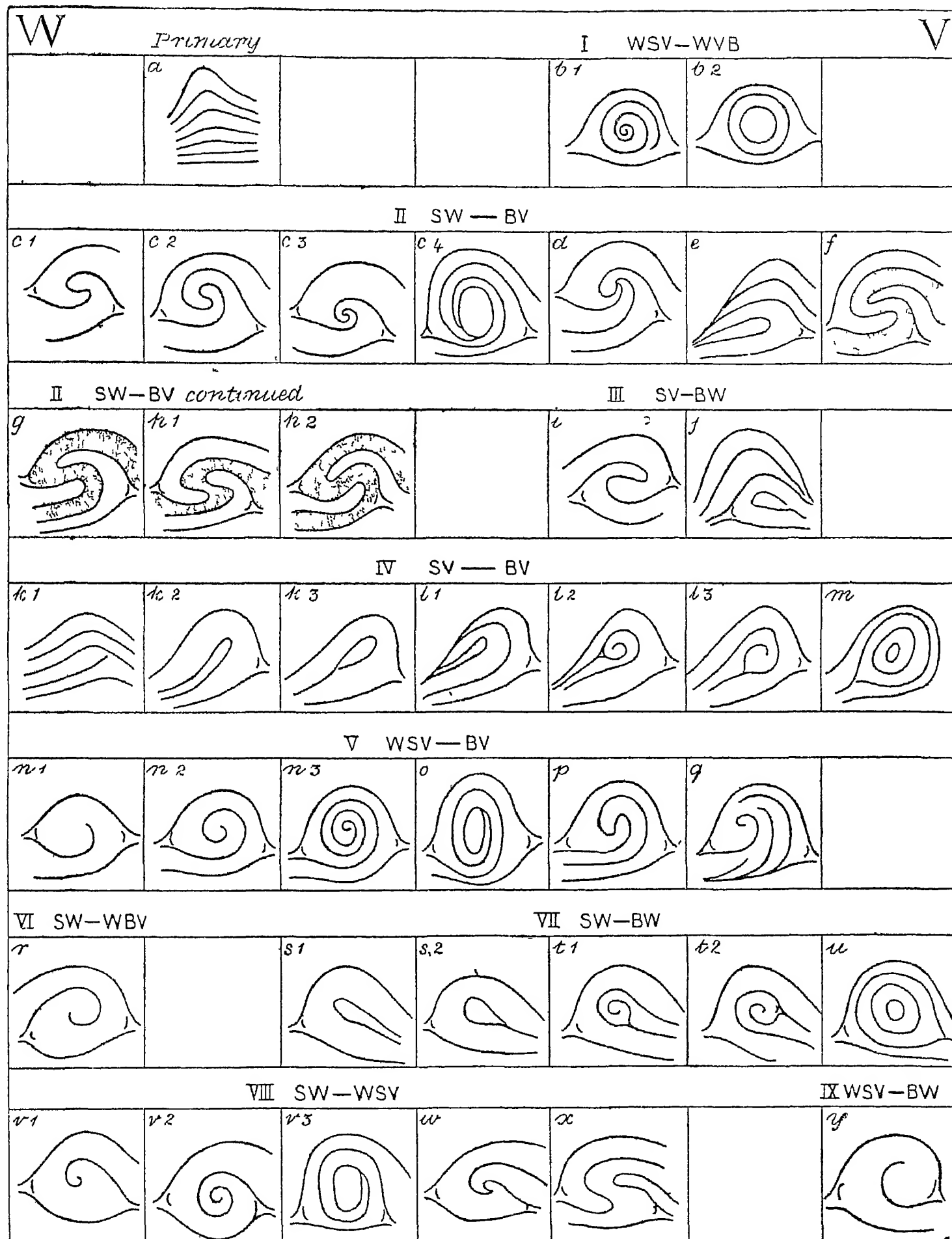


is absent, then following those that diverge from the other (see also figs 2, 3, 4) As ridges are apt to bifurcate, to join with others, and also to end abruptly, it is necessary to follow a consistent course in such cases. In bifurcations the innermost branch should be followed. Whenever a ridge ends, the pencil should stop also, and recommence on a new ridge, selecting that which appears to continue the direction of the former one in the truest way. In case of doubt, the pencil should, as before, follow the innermost of the two lines between which the doubt lies. If opposite rules to these were imposed, the outline would be much less speedily analysed, and be by no means so simple when completed. The sudden transformation of a maze of ridges into an orderly pattern by this easy process is truly remarkable.

I outlined, where necessary, or otherwise examined, more than 1000 photographically enlarged impressions with much care, and found, on sorting them, that nearly all their patterns fell satisfactorily into one or other of the divisions in fig 9, where twenty-five main divisions are arranged, according to the ten classes already described, namely, the primaries and the nine others. It must, however, be understood that, in sorting the impressions, no regard was paid in the first instance to other than essential points of difference. After this was done, some little regard was bestowed on secondary points, and a few of the species were subdivided by adding the numbers 1, 2, 3, &c, to their descriptive letter. For example, species *c* is subdivided into four groups, *c* 1, *c* 2, *c* 3, *c* 4, according to the amount of twist of the two belts of ridges of which it is composed, and to the presence or absence of a nucleus.

Marked instances of the occasional interpolation of a belt of ridges running from one side to the other through the pattern, and in a more or less tortuous course, occur in Class II. and correspond to the forms *f*, *g*, *h* 1, *h* 2. Such a belt often exists, but it is usually too narrow or ill defined to be worth regard. A pattern is sometimes composed altogether of such a tortuous belt, in which case it would rank along with the Primaries in Class *a*. As there are twenty-six letters of the alphabet, and only

Fig 9.



twenty-five of them are used in fig 9, the last letter, *z*, will serve to show that any pattern to which it is attached is *not* one of those in fig 9.

All the patterns in fig 9, are drawn on the supposition that W lies to the left and

V to the right. They are therefore those of impressions made by the left thumb, or of the ridges themselves as seen on the right thumb. The patterns must be read in a reversed sense, such as they would appear in a looking glass, to be applicable to impressions from the right thumb, or to the ridges themselves as seen on the left thumb.

Without professing to present a very complete epitome of the varieties, this table, (fig 9) certainly provides a serviceable one, and may be looked upon as a convenient first step towards a more elaborate performance (fig 8 would rank in it as *j* if *W* lay to the left, as *e* if it lay to the right)

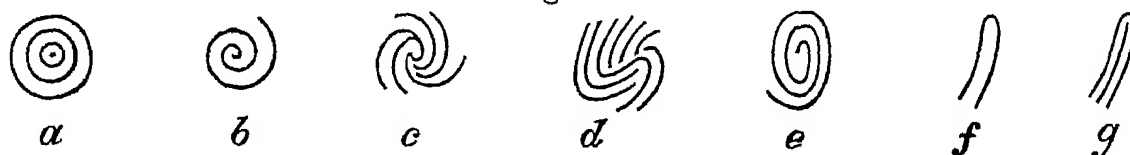
It must not be supposed that the occurrence of each of these representative patterns is equally frequent, such is very far indeed from being the case. The proportion of all the cases that falls under each of the ten classes varies between 1 and 65 per cent. About one half of all the specimens are of the pattern shown at *k* 2, which I call a *loop*, and nearly 25 per cent are of one of those described as *c*.

It was mentioned that the descent of all the patterns can be traced from the primary. The first step in the evolution of the loop is seen in *k* 1, and that of the whorls is usually through the loop, as in *l* 1, *l* 2, &c., but sometimes it proceeds directly

#### *Nuclei.*

The nucleus of a pattern may be of many varieties, and its form arrests the attention. I give a few diagrammatic patterns of the nuclei of whorls (*a* to *e*, fig. 10). Those of the loops present fewer varieties, the two principal of which are a central furrow, *f*, or a central ridge, *g*.

Fig 10.



#### *Exhibited Specimens.*

I exhibit numerous impressions with or without the outlines of the patterns drawn upon them, some are photographically enlarged, others are impressed in printer's ink on glass, for use in the optical lantern. Besides these I exhibit some of the principal ways of making the impressions, as by first pressing the thumb or finger upon a piece of smoked glass, porcelain or mica, and then by transferring part of the soot that adheres to the ridges, to paper whose surface is gummed, sized, or varnished. I show also, a very convenient pocket apparatus for taking impressions at any time with printers' ink. I borrowed the main idea of this from Sir W. J. HERSCHEL.

#### *Identifying Patterns.*

In identifying a pattern, we must bear in mind that the thumb which makes the impression is not a rigid body of invariable size and shape, but that the patterns it

impresses at different times will vary. If those times are separated by long periods of growth or decay, the patterns may become much distorted. They may change their shape just as the pattern on different portions of the same piece of machine-made lace may become variously stretched by wear, or shrunk by wet, or even be torn. In comparing the patterns on two such portions, the evidence of their identity would chiefly lie in the number of threads that went to the making of corresponding parts of the pattern of the lace. So, in the impression of the thumb marks, the first point is to count the number of ridges that intervene between such points in the pattern as we may be able to define with sufficient precision for the purpose. The simplest way of doing this for descriptive purposes, would be to mark a few appropriate points on each of the patterns in fig. 9 with the letters, A, B, C, &c. Then it would give a clear description of the larger peculiarities of a particular pattern, to say that it was of the general pattern so and so, and that the number of ridges between A and B, C and D, &c., was so and so, respectively. I shall have occasion in this paper to use two methods of reference and measurement, which had best be described now.

First, suppose V and W both to exist (fig. 2). Then join VW, bisect it at M and draw a perpendicular through M, meeting the upper boundary in T and the lower in I.

Secondly, suppose only V to exist (fig. 3). In this case the curve must be of the loop form, which almost always has a well marked axis determined by the direction of the upper end of the innermost bend of the loop. There is usually quite enough length in a straight line of the uppermost portion of the inner bend to indicate the direction of the desired axis, which meets the upper boundary of the pattern at A, and the lower at I. Let fall a perpendicular from V on to this axis, cutting it at O, and meeting the opposite boundary at Y.

Thirdly, suppose only W to exist. Then proceed just as before, substituting the letter W for V, and calling the point where the prolongation of WO meets the opposite boundary, by the letter X instead of Y.

The cross lines in these three figures will serve the same purpose as the cross lines of the compass card marked upon a map. In two of the three cases W is present, which letter, since it suggests west, may be designated by the numeral 24, which is the number expressing the west point of the compass, N being 0 (or 32), and S being 16.

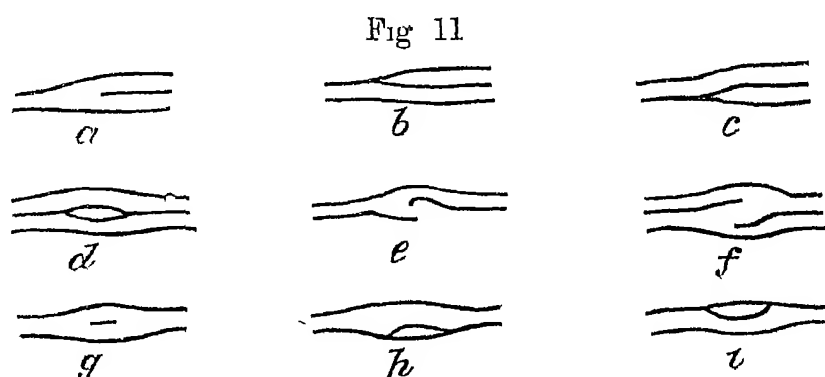
In the other two cases V is present. By parity of nomenclature V would always be designated by 8. Then T or A, as the case may be, is designated by 0 (or 32), and U or I by 16. The intermediate points will be numbered accordingly. This nomenclature, it will be observed, serves equally well for the right or left thumb, and for either direct or reversed impressions of them.

### *Identifying Minutæ.*

The patterns on the thumb have just been compared to those on lace which may be variously shrunk or stretched, but in which the number of threads that are used to form each detail of the pattern remains unaltered. The simile may be further

extended by supposing the thread to have been variously irregular and divided. Then the position of its several irregularities in respect to the parts of the pattern would remain unchanged, although the shape of the piece of lace as a whole may have greatly altered.

The minutæ about to be described form minor patterns of their own, quite distinct from the larger patterns shown in fig 9. They are chiefly connected with the commencements of interpolated ridges. At or about a particular spot in the pattern two ridges that had previously run in parallel and adjacent courses are replaced by three ridges (fig 11). This is the main fact to be noticed. The particular way in which



the two ridges seem to have been converted into three is by no means so important, because its appearance is often false and misleading. The conversion may have been affected either by a new ridge arising between two others which diverge so as to yield place to the intruder, as in fig. 11*a*, or else by one of the two ridges bifurcating, as in *b* and *c*.

But grave difficulties not unfrequently arise in distinguishing between these three cases. One impression may show one form, and another impression taken immediately afterwards from the same thumb may show another. The reason is that the ridges are not of a uniform height and that the head of the fork is often low, and fails to leave its mark on one of the prints, though it does so on the other. Thus neither of the two cases *b* and *c* admits of being certainly distinguished from *a*. This kind of difficulty is frequent where a ridge momentarily divides so as to enclose a small crater as in *d*. One lip of the crater may leave no mark, and the impression of *d* might have the appearance either of *e* or of *f*. Similarly as regards islands, as in *g*, *h*, and *i*.

These remarks are intended as a caution against placing too much trust in the specialities of these appearances, though usually the distinction between a fork and the beginning of a new ridge is clear enough.

#### *Persistence of Patterns.*

I submit the impressions in Plate 1 in justification of the conclusions to be drawn from them. They were all furnished to me by the kindness of Sir W. J. HERSCHEL, who, when employed in the Indian Civil Service in Bengal many years ago, introduced in his district the practice of taking impressions from the first two fingers of the

right hands of witnesses and others as a check against personation. I also possess photographs of some other impressions besides those in Plate 1, taken from other fingers of some of the same persons, and which tell a similar tale.

Each of the eight double sets in Plate 1 consists of two impressions of the same digit of the same person, taken at the beginning and end of a long interval of years. In six of the eight double sets the impressions are those of two different fingers of three different persons. In the remaining two the impressions are of one finger of two different persons. The entry 1 *r* means the forefinger of the right hand, 2 *r* its middle finger, 3 *r* its third finger. The cases 1 and 2 refer to a youth who was a child of seven and a half years old when the first impression was taken, this was nine years previous to the second impression. The remaining six cases refer to four men who were adults when the first impression was taken, and this occurred at a period varying between twenty-eight and thirty-one years before the second impression. The photographs of all these impressions are enlarged to twice their natural size for the greater convenience of reference, and every point suitable for comparison in each pair of impressions has been examined and noted in Plate 2. It is rare that the one impression presents quite the same portion of the pattern as its fellow. Also it occasionally happens that a portion of one impression is blotted or otherwise too imperfect to allow of fair comparison with the corresponding portion of the other. Subject to these necessary restrictions every fork, junction, crater, or island in each impression has been noted, and in every single case has been found to occur in both the members of the same pair, subject only to the reservations previously made, that is to say, what appears as a fork in a first impression sometimes appears as the independent interpolation of a new ridge in the second, or *vice versa*. I have in these cases reckoned it as being of similar appearance in both, and have marked it with the same symbol in both of the skeleton charts, viz, by a fork or by a dot, selecting between the alternative symbols the one that appeared on the whole to be most suitable.

No on the Plate	Initials	Digit	Age at date of first impression	Date of the first impression	Date of the second impression	No of years interval	No of beginnings and ends of ridges	No of forks and junctions of ridges	Total No of points of comparison
1	A E H	1 <i>r</i>	7½	1881	1890	9	19	14	33
2	A E H	3 <i>r</i>	7½	1881	1890	9	18	18	36
3	N H T	1 <i>r</i>	adult	1862	1890	28	16	11	27
4	N H T	2 <i>r</i>	adult	1862	1890	28	17	19	36
5	F K H	1 <i>r</i>	adult	1862	1890	28	27	28	55
6	R F H	2 <i>r</i>	adult	1859	1890	31	10	17	27
7	W J H	thumb <i>r</i>	adult	1860	1890	30	18	32	50
8	W J H	3 <i>r</i>	adult	1859	1890	31	15	17	32
Grand totals . . . . .							140	156	296



I did my best to justly reckon the number of minutæ in each impression that admitted of comparison, but found it difficult, perhaps it is impossible to be absolutely accurate

Other persons may make estimates that differ slightly from mine, but mine are, I am sure, substantially correct and trustworthy for all practical purposes. I counted as separate points both of the ends of every island, however short the island might be, and both of the forks that enclosed every crater however minute.

The upshot of a careful step by step study is that I have found an absolute and most extraordinary coincidence between the details of each of the two impressions of the same finger and of the same person. There was, as the table shows, a grand total of no less than 296 (say, roundly, 300) points of comparison, and not a single one of them failed, though I had much trouble in deciphering the ridges, especially about the V-point in case 5. There was no one case found of a difference in the number of ridges between any two specified points. Never during the lapse of all these years did a new ridge arise, or an old one disappear. The pattern in all its minute details persisted unchanged, and, *à fortiori*, it remained unchanged in its general character.

[January 28. Since writing this memoir, I have had opportunities of making a considerably larger total of comparisons between other pairs of impressions, and I have thus far found one instance, and one instance only, of any fundamental disaccord. It was a ridge that had been partially cleft in a child, but when he had grown into a boy the cleft had disappeared.]

The comparison would, however, present discrepancies and be much less effectively carried on if it were performed by first registering the observed peculiarities of one pattern, next those of the other, and, lastly, comparing the two registers. Each would be likely to contain points in which the other was deficient, and not a few very characteristic features might be overlooked in both. For example it will be seen in the two impressions, No 2 in the skeleton chart, that I have inserted an arrow head to draw attention to a small spot a little in front of it, which represents an isolated papilla. This spot would have been passed over as a mere accident of the ink, unworthy of record, had it not been that, in making the comparison from point to point, the same dot was observed in both impressions. It was then recognised to be of importance. It is pretty to notice how the small dot in the child has grown to a larger dot in the youth.

The lapse of about thirty years is seen in these eight examples to have introduced no fundamental difference in the patterns of four different adults, nor has the lapse of nine years, during the period of growth from childhood to youth, done so in a fifth person. The patterns often have become broadened and variously distorted, especially in case 6; but in respect to those characteristics, on which alone I have laid any stress, there has been no change whatever.

It appears that the ridges make their first appearance in the fourth month of foetal

life, and to be fully and finally developed in the sixth month, for they then seem to possess the same degree of complexity of structure that exists in the patterns of adults. Putting all together, we may fairly infer that, from birth to death, there is no change in the fundamental characteristics of the thumb and finger patterns, nor can there be any after death up to the time when the skin perishes through decomposition.

The popular idea that has hitherto been jumped at, without adequate evidence,\* is now shown to be strictly correct on very good evidence and after careful inquiry. There appear to be no means of personal identification other than deep scars and tattoo marks, comparable in their permanence and certainty with those of the thumb and finger marks. All the dimensions of the limbs alter in the slow course of growth and decay. The colour of the hair, the quality and tint of the skin, the expression of the features, the gestures, the handwriting, even the eye colour, change after many years. There seems to be no persistence anywhere in the bodily structure, except in these minute and too much disregarded papillary ridges.

### *Scars*

The question remains to be considered as to how far the patterns may be affected by scars, or obliterated by rough usage. I find that, of the 2500 or more persons whose thumbs have been impressed at my small Anthropometric Laboratory at South Kensington, the patterns are rarely destroyed to any considerable degree. I have to search through hundreds of thumb marks to find an instance of even a small scar. Partial obliterations are more frequent, but here, though much is lost, a sufficiency remains; and if the thumb is rolled and not only pressed, more would be available. If the fingers had been rolled in making the impressions in Plate 2, there would have been perhaps twice as many points of comparison, for the areas they represent would have been twice, or nearly twice as great as they are now, and the number of points suitable for comparison would have been proportionately increased.

### *Analogy between the Classes and Ordinary Genera.*

We have seen that the peculiarities which distinguish the classes of the patterns are fundamentally distinct. It might thence be inferred that the class of any given pattern would be clearly distinguishable. But this is not invariably the case. A characteristic, however fundamental in its character, may be so poorly developed in a particular case, as to be overlooked, or be barely, if at all, traceable.

\* Subsequent inquiry confirmed the opinion expressed in my lecture at the Royal Institution, referred to above, that an often repeated assertion to the effect that impressions of the hand are used in Chinese prisons for purposes of identification, is erroneous. The impression of the finger in China, as elsewhere in the East, is sometimes affixed to documents merely as a ceremony of personal contact, much as the witnesses in an English court of law are required to hold and to kiss the Bible on which they are sworn.



A core as in *b2*, fig 9, belongs to a WSV—WBV class, while a core that is enclosed in a loop, as *m*, belongs to a SV—BV, or one as *u*, to a SW—BW class. But the enveloping loop may be so narrow as to be overlooked. Nay, it may consist of but a single ridge, and that ridge may not make the complete circuit, but either stop by the way or form a junction with the outer ridge of the core. Transitional cases of this sort may and do occur, and they might conceivably occur frequently.

There are perhaps no two classes that might not be in some way connected by transitional cases, though it may often be difficult to imagine how. We are not justified in denying either the possibility or the frequency of any such transitional form on purely *a priori* grounds, but must appeal to observation, which assures us that they are rare.

In order to rightly understand the degree and the way in which any class of pattern is isolated, it is necessary to study a large number of specimens, consequently, as loops are so numerous, we cannot do better than to base the discussion upon them, and learn whether or no the individual variations of loops cluster around a central or typical form, or whether they are distributed in any other way. We must study the peculiarities of the loop separately and in detail, and the best detail for our purpose is the number of ridges in AH, where H is the point in the innermost bend of the loop at which it is cut by AI (see figs. 3 and 4)

The ridges in AH are easily counted because AH cuts them squarely, owing to the construction of the figure. I took a number of specimens of loops, in the order in which they came to hand, and had the number of ridges in AH counted in each loop. (I had also, myself, previously made more than one independent trial on a considerable scale, but the specimens had not been those of a strictly random selection, and I thought best not to use them)

The ridge at A was counted as 0, the next ridge as 1, and so on up to H. Whenever the line AH passed across the neck of a bifurcation, so that there was one ridge fewer on one side of the point of intersection than on the other, there would clearly be doubt whether to reckon it as 1 or as 2 ridges. A compromise had, therefore, to be made by counting it as  $1\frac{1}{2}$ . After the number of ridges in AH had been counted in each case, all residual fractions of  $\frac{1}{2}$  were alternately treated as 0 and as 1. In a very few cases there was doubt whether to classify a pattern that approximated to  $k+1$ , as a loop, the number of whose ridges in AH was 0, or even 1, or whether to consider it as a Primary, *a*.

It is more convenient to work from the results when given in the form of the percentages, which will be found in Table I, and where the number of cases from which the percentages were made is entered at the top. It is quite unnecessary to work more closely than to the nearest integer. We see at a glance that the different numbers of ridges in AH do not occur with equal frequency, that 1 ridge is a rarity, and so are cases of ridges above 15 in number, but that the cases are frequent of 7, 8, and the neighbouring numbers of ridges. There is clearly a rude sort of order in

their distribution, the cases being more numerous for median values, and tailing away into nothingness at the top and bottom of the column. A vast amount of statistical analogy assures us that the orderliness of the distribution would be increased if the cases observed had been much more numerous. Later on this inference will be corroborated. There is a sharp inferior limit to the numbers of ridges, because they cannot be less than 0, but independently of this, we notice the growing infrequency of small numbers as well as of large numbers of them. There is no strict limit to the latter, but the trend of the figures convinces us that say, 40 or more ridges in AH are practically impossible. Therefore, no individual number of ridges in AH can possibly depart very widely from the observed average numbers of ridges in AH, but the range of possible departures is not sharply limited, except at its lower margin. Their possibilities are not "rounded off," to use a common but very misleading expression that is often applied to the way in which genera are isolated. The range of the possible departures in the case of genera is not suddenly and sharply restricted, but the rarity of the stragglers from the average form rapidly increases with the degree of their departure, until no more of them are met with.

TABLE I

No of ridges in AII	No of cases reduced to per cents		VY/OI	No of cases reduced to per cents		AO/AH	No of cases reduced to per cents	
	Left	Right		Left	Right		Left	Right
	171 cases	166 cases		149 cases	140 cases		176 cases	163 cases
1	.	1	03-04	2	3	01-02	1	2
2	1	2	05-06	11	8	03-04	3	7
3	3	2	07-08	14	9	05-06	3	11
4	5	2	09-10	18	21	07-08	9	9
5	5	3	11-12	23	16	09-10	15	22
6	18	4	13-14	7	24	11-12	13	15
7	14	8	15-16	10	8	13-14	12	12
8	16	8	17-18	6	3	15-16	14	11
9	10	11	19-20	6	5	17-18	10	8
10	8	9	21-22	1	1	19-20	5	1
11	10	14	above	2	2	21-22		
12	8	11				23-24	6	1
13	2	10				25-26	4	
14		7				27-28	3	
15		6				29-30	1	
above		2				above	1	1
	100	100		100	100		100	100

It is convenient to discuss these and similar cases in the way adopted in Tables II and III. These show how far the distribution of the observed cases conforms to the well-known theoretical law of Frequency of Error. If they conform to it fairly well, we are justified in speaking of a central or typical number of ridges in AH, and of considering any other number of ridges as a departure from that typical and central value.

TABLE II.

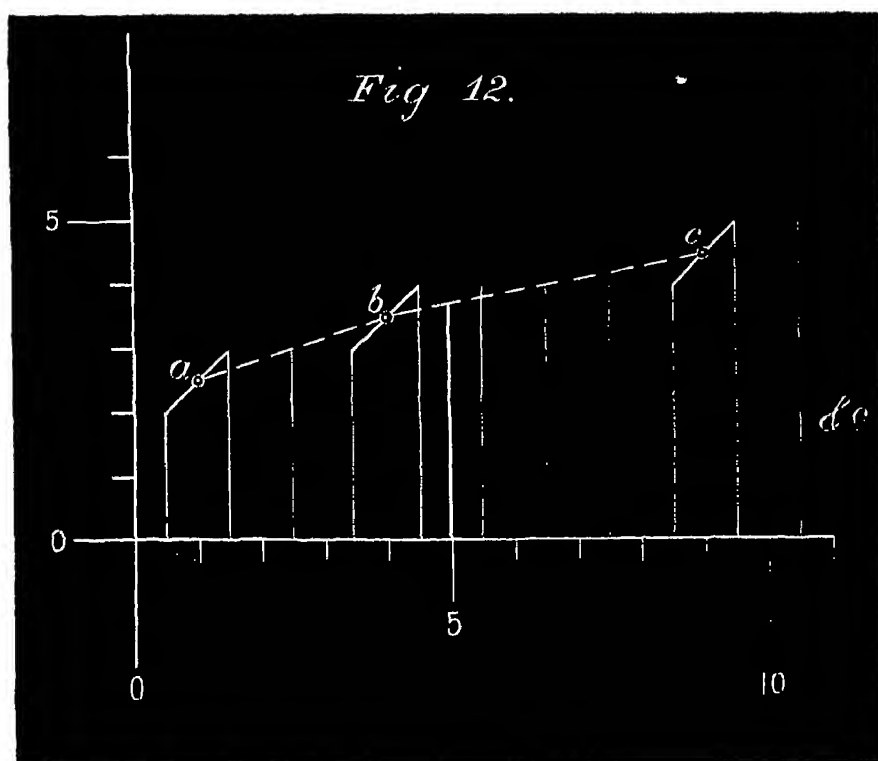
Abscissæ reckoned in centesimal parts of the interval between the limits of the scheme 0 to 100	Ordinates to the six schemes of Distribution, being the ordinates drawn from the base of each scheme at selected centesimal divisions of the base											
	No of ridges in AH				Values of VY/OI				Values of AO/AH			
	Left		Right		Left		Right		Left		Right	
	Observed	Calculated from $M=78$ $p e = 1.9$	Observed	Calculated from $M=104$ $p e = 2.3$	Observed	Calculated from $M=110$ $p e = 0.31$	Observed	Calculated from $M=115$ $p e = 0.25$	Observed	Calculated from $M=136$ $p e = 0.36$	Observed	Calculated from $M=108$ $p e = 0.30$
5	3.8	3.2	3.8	4.8	0.49	0.35	0.54	0.54	0.58	0.48	0.36	0.32
10	4.8	4.2	5.5	6.0	0.59	0.51	0.64	0.67	0.74	0.68	0.50	0.48
20	5.8	5.4	7.3	7.5	0.78	0.71	0.85	0.84	0.96	0.91	0.66	0.67
25	6.1	5.9	7.9	8.1	0.83	0.79	0.91	0.90	1.00	1.00	0.79	0.75
30	6.4	6.3	8.5	8.6	0.89	0.86	0.99	0.95	1.04	1.08	0.87	0.82
40	7.1	7.4	9.5	9.5	1.00	0.98	1.05	1.05	1.21	1.22	0.98	0.93
50	7.8	7.8	10.5	10.4	1.10	1.10	1.15	1.15	1.37	1.36	1.04	1.05
60	8.4	8.2	11.3	11.3	1.18	1.22	1.29	1.25	1.48	1.50	1.18	1.17
70	9.3	9.3	12.1	12.2	1.32	1.34	1.33	1.35	1.66	1.64	1.31	1.28
75	9.9	9.7	12.5	12.7	1.46	1.41	1.41	1.40	1.73	1.72	1.39	1.35
80	11.0	10.2	13.0	13.3	1.53	1.49	1.45	1.46	1.90	2.81	1.48	1.43
90	11.5	11.4	14.3	14.8	1.73	1.69	1.77	1.63	2.23	2.04	1.69	1.62
95	12.2	12.2	15.0	16.0	1.80	1.85	2.00	1.76	2.48	2.24	1.81	1.78
									about			

TABLE III

Abscissæ reckoned in centesimal parts of the interval between the limits of the curve  0 to 100	Ordinates to the six curves of distribution drawn from the axis of each curve at selected centesimal divisions of it They are here reduced to a common measure, by dividing the observed deviations in each series by the probable error appro- priate to the series and multiplying by 100 For the values of M, whence the deviations are measured, and for those of the corresponding probable error, see the headings to the columns in Table II						Mean of the corresponding ordinates in the six curves after reduction to the common scale of p e = 100 965 observations in all	Ordinates to the normal curve of distribution, probable error = 100.
	No of ridges in AH		Values of VY/OI		Values of AO/AH			
	Left	Right	Left	Right	Left	Right		
5	-211	-291	-196	-244	-217	-230	-231	-244
10	-158	-213	-164	-204	-172	-183	-182	-190
20	-105	-135	-103	-120	-111	-130	-117	-125
25	-84	-109	-87	-92	-100	-87	-93	-100
30	-74	-83	-68	-64	-89	-60	-73	-78
40	-37	-44	-31	-44	-42	-23	-37	-38
50	0	+4	0	0	0	0	+1	0
60	+31	+39	+23	+56	+33	+43	+38	+38
70	+79	+74	+68	+72	+83	+87	+77	+78
75	+116	+91	+116	+104	+103	+113	+107	+100
80	+168	+113	+138	+120	+150	+143	+139	+125
90	+200	+170	+203	+248	+242	+213	+213	+190
95	+231	+200	+225	+340	+311	+253	+260	+244

The method used here is one that I have often described, but I fear I must briefly describe it again because it is not generally understood, though it is already beginning to be used by anthropologists and others. The 100 cases (the percentages in Table I) that refer, say, to the left thumb are entered upon a piece of paper ruled by 101 vertical lines, numbered from 0 to 100, which divide any horizontal line into 100 equal and horizontal spaces. It appears from the table that we may have to deal with various numbers of ridges from 0 up to 15, so there must be 16 horizontal lines at equal distances apart, and numbered from 0 to 15, enclosing 15 equal vertical spaces.

The table begins by telling us that out of the 100 cases there are 1 of two ridges, 3 of three ridges, 5 of four ridges, and so on. These values are entered on the ruled paper by erecting, (fig. 12,) one ordinate reaching to the second line in the middle of the



first space, three ordinates reaching to the third line and severally standing in the middle of each of the next three spaces (which, counted from the beginning, are the second, the third, and the fourth), five ordinates reaching to the fourth line and severally standing in the middle of each of the next five spaces, and so on, until all the 100 spaces have been utilized for the 100 tabular entries. Then a curve may be drawn with a free hand through the tops of the 100 ordinates, and the figure called a Scheme of Distribution is thereby produced. But there is an objection to free hand curves, in the temptation to draw them too smoothly. Therefore I do no more than unite with straight lines, as shown in fig 12, the halfway points *a*, *b*, *c*, &c between each successive step. The 100 ordinates have now served their purpose, and being in the way, had better be rubbed out (practically they are never drawn), leaving only the curve, the divisions between which the ordinates were or were supposed to be drawn, and the side scale.

New ordinates to the curve are now erected at the convenient divisions of the base

given in the first columns of Tables II. and III. (see the broad white line corresponding to 5 in fig 12). They are measured, and their lengths are recorded, and may at any future time be again mapped down in order to form a skeleton by which to reproduce the original scheme. The lengths of these interpolated ordinates are given in the column of Table II headed "Observed." Being interpolations, they do not consist, except by chance, of an integral number of ridges. But fractional values are not meaningless, they have already been employed whenever AH cuts the neck of a fork.

The ordinate at the 25th division of the base, called  $Q_1$ , cuts off the lower quarter of the scheme, the ordinate at the 75th, called  $Q_3$ , cuts off the upper quarter. Half the difference between them, or  $\frac{1}{2}(Q_3 - Q_1)$ , is called the Quartile, and is expressed by  $Q$ . It measures the "probable" dispersion (in the sense of "probable error") of individual values from the value of  $\frac{1}{2}(Q_3 + Q_1)$ , which is called  $M'$ .

In a symmetrical curve  $M'$  is identical with the ordinate at the 50th division, in other words, with the median value of all the ordinates in the series, and is called  $M$ . Further, in a symmetrical curve, the median  $M$  is identical with their arithmetic mean value. In the six different series contained in Table II., and in numerous analogous ones that I have worked out elsewhere, the values of  $M'$  and of  $M$  are nearly identical. Whenever they differ, I have taken an intermediate value that is nearer to  $M$  than to  $M'$ . This correction has been always very trifling. The values of  $M$  and  $Q$  for each of the series with which we are concerned, are given at the heads of the second of each pair of columns in Table II.

The next step is to change from the Scheme to the Curve that bounds it; the ordinates are measured henceforth from the axis of the curve, up or down as the case may be. The axis is a line drawn parallel to the base of the scheme, which cuts the curve at the point where it was met by  $M$ ; that is by the ordinate erected at the 50th division of the base.

The axis is divided into 100 divisions just like the base. The ordinates of a curve of this description, not founded on any observations, but wholly on the theoretical law of Frequency of Error, can be deduced from the well-known tables of the Probability Integral. They, and the curve itself, may be conveniently spoken of as "Normal."

The few ordinates of the normal curve with which we are concerned will be found in the last column of Table III. There the quartile (= probable error) is taken as 100 and not as 1, in order to avoid decimals in the tabular entries, which are restricted to three figures each.

When preparing to compare the ordinates of a curve drawn from observation with those of a normal curve, we must first multiply the ordinates of the normal curve, whose quartile (or probable error) = 100, by the value of the quartile of the observed curve. Or, conversely, if we wish to compare the ordinates of the normal curve whose

quartile = 100, with those of the observed curve, we must first divide those of the observed curve by the value of their own quartile, and then multiply them by 100. The latter process has been adopted in Table III

There is yet another useful step. Given the values of  $M$  and  $Q$  we may calculate the value of any ordinate in the scheme, by the help of the values of the normal ordinates to the curve given in the last column of Table III., and collate the calculated with the observed values. This has been done in Table II

We will first consider the results shown in Table II. It is seen that the accordance between the calculated and observed number of ridges in  $AH$ , in the left and in the right thumbs severally, is respectably close. Considering the paucity of the observations, which are only 171 in the one case and 166 in the other, there is nothing in the results that contradicts the possibility of a much closer conformity when very many more observations are dealt with.

Precisely the same process has been gone through in respect to the values of the fractions of  $VY$  divided by  $OI$  (see fig 3), which is practically the breadth of the loop divided by its length. The results are of a similar character to those yielded by the numbers of ridges in  $AH$

Again, I have tried the fraction of  $AO$  divided by  $AH$ , and still the results are found to be of the same kind

Now turning to Table III. I there obtain a general average result from all of the three double sets, by an artifice. Each observed series of departures from the axis of the curves is reduced to what it would have been if the unit of the scale by which its departure had been measured, was equal to its own quartile multiplied by 100. In short, every one of the ordinates in each series was divided by the value of the quartile of that same series, and then multiplied by 100. Their average results are given in the last column but one, and the corresponding normal values in the last column. The orderly run of the figures is much closer now than it was in any one of the six separate series because they are derived from many more observations, namely, 965 of them.

We also see that though there is an obvious want of exact symmetry in the ordinates of the observed curve, their general accord with those of the normal curve is very fair. It is quite close enough to establish the general proposition that we are justified in relying upon the ideal conception of a typical form of loop, different for the two thumbs, from which individual loops differ. That the departure from the typical form is usually small, rarely rather greater, and very rarely indeed rather greater still.

It would be tedious to enumerate the many different trials that I have made for my own satisfaction, in order to assure myself that the variability of the several patterns was really of the quasi-normal kind just described. In my first trial I measured in various ways the dimensions of about 500 enlarged photographs of loops, and about as many of other patterns, and found that the measurements in each and every case

formed a quasi-normal series. I do not care to submit these results, because they necessitate more explanation and analysis than the interest of the corrected results would, perhaps, justify, to eliminate from them the effect of variety of size of thumb, and some other uncertainties. Those measurements referred to some children, a few women, many youths, and a fair number of adults, and allowance has to be made for variability in stature in each of these classes.

The proportions of a typical loop are easily ascertained if we may assume that the most frequent values of its variable elements, taken separately, are the same as those that enter into the most frequent combination of the elements taken collectively. This would necessarily be true if the variability of each element separately, and that of the sum of them in combination, were all strictly normal, but as they are only quasi-normal the assumption must be tested. I have done so by making the comparisons shown in Table IV., which come out correctly to within the first decimal place.

TABLE IV.

	Left thumb	Right thumb.
(a) Median of all the values of VY	10.1	12.5
(b) Median of all the values of OI	8.9	10.1
Value of $a/b$	1.11	1.24
Median of all the fractions $VY/OI$	1.10	1.15
(c) Median of all the values of AO	4.6	4.6
(d) Median of all the values of AH	3.3	4.4
Value of $c/d$	1.40	1.05
Median of all the fractions $AO/AH$	1.36	1.08

They show that it is practically the same thing whether we take the fraction, which is the median of all the fractions, or whether we take the fraction whose numerator is the median of all the numerators, and whose denominator is the median of all the denominators. I have used the medians here and throughout this inquiry instead of the arithmetic means, but an inference like the foregoing which is based on the medians, may be accepted without cavil as being equally true of the means.

This being premised, the proportions of the typical loop are to be taken as follows:—



	Left thumb	Right thumb
Length of OA in millimetres	4.6	4.6
OI       "	8.9	10.1
OV       "	7.6	8.3
OY       "	3.1	4.2
AH       "	3.3	4.4
Number of ridges in AH	7.3	9.9
Mean breadth of one of the ridge intervals in AH	0.46	0.45

As absolute measures, the above are too small for the average adult male and too large for the average adult female, but as proportions they are correct.

I do not see my way to discuss the primaries on the same general lines as the loops, because they possess no distinct points of reference. But their general appearance does not give the impression of clustering around a typical centre. They seem rather to suggest the idea of the head of a stream, that begins to diverge from the first.

As regards other patterns, I have made many measurements altogether, but the specimens of each sort were comparatively very few, except in *c* patterns. In all cases where I was able to form a well-founded opinion, the existence of a typical centre was indicated. It was not necessarily or usually the same in the two thumbs, indeed, there is a curious difference between their patterns, into which I do not propose to enter here.

There is reason to believe that the patterns are hereditary. I have no adequate amount of data whereby to test the truth of this belief by a direct inquiry, but rest the belief partly on analogy, but more especially on the ascertained existence of a considerable tendency to symmetry. When, for instance, there is a primary pattern on one thumb, there are not far from ten chances to one in favour of its being found on the other. Again, if there is a loop in one thumb, there is a strong chance that it will be found in the other thumb also. Similarly as regards each pair of corresponding fingers. Therefore the causes of the pattern must not be looked for in purely local influences. Part of the causes why it and not another pattern is present, are common to both sides of the body and may therefore be called constitutional, and be expected to be hereditary.

Accepting, then, the hypothesis that the patterns are to some extent hereditary, we possess in them an instructive instance of the effects of heredity under circumstances in which sexual selection has been neutral. The very existence of the patterns has been hitherto almost overlooked, because they are too small to attract attention, or thought too uninteresting to notice. Neither do they appear to be correlated with any desirable or repellent quality. It is true that the breadth of a ridge-interval may afford a direct indication of the delicacy or the reverse of the sense of touch, as measured by the just discernible distance between compass points, and some indirect indication of the sensibility generally. (I do not know that it is, but have planned



experiments for testing the supposition.) Yet, even if so, the fact would have no bearing on the attractiveness or otherwise of any particular pattern, because the form of a pattern has nothing to do with the fineness or coarseness of the ridges that compose it. There has, therefore, been complete promiscuity of marriages, or, as it is now called, panmixia, in respect to these patterns. We might consequently have expected them to be hybridised. But that is most assuredly not the case; they refuse to blend. Their classes are as clearly separated as those of any of the genera of plants and animals, while we happen to know enough about their origin to understand that this must be the case, inasmuch as they are intrinsically different. Each of the patterns keeps as pure and distinct from the others as if they had been severally descended from a thorough-bred ancestry, each in respect to its own peculiar form.

As regards the influence of all other kinds of natural selection, we know that they co-operate in keeping races pure by their much more frequent destruction of the individuals who depart the more widely from the typical centre. But natural selection is wholly inoperative in respect to individual varieties of patterns, and unable to exercise the slightest check upon their vagaries. Yet, for all that, the different classes of patterns are isolated from one another, through the rarity of transitional cases, just as thoroughly, and just in the same way, as are the genera of plants and animals. There is no statistical difference between the form of the law of distribution of individual patterns about their respective typical centres, and that of the law by which, say, the Shrimps described in Mr WELDON'S recent memoir ('Roy. Soc. Proc.,' vol. 47, p. 445) are distributed about theirs. In both cases the distribution is in quasi-accordance with the theoretical law of Frequency of Error, and this form of distribution is caused in the case of the patterns entirely by internal conditions, and in no way by natural selection in the ordinary sense of that term.

It is impossible not to recognise the fact so clearly illustrated by these patterns in the thumbs, that natural selection has no monopoly of influence in forming genera, but that it could be wholly dispensed with, the internal conditions acting by themselves being amply sufficient to form them. When the internal conditions are in harmony with the external ones, as they appear to be in all long-established races, their joint effects will curb individual variability more tightly than either would do by itself. The normal *character* of the distribution about the typical centre will not be thereby interfered with. The probable divergence (= probable error) of an individual taken at random will be lessened, and that is all.

Not only is it impossible to substantiate a claim for natural selection that it is the sole agent in forming genera, but it seems, from the experience of artificial selection, that it is scarcely competent to do so by favouring mere *varieties*, in the sense in which I understand the term.

My contention is that it acts by favouring small *sports*. Mere varieties from a common typical centre blend freely in the offspring, and the offspring of every race whose statistical characters are constant, necessarily tend, as I have often shown, to

revert towards their common typical centre Sports do not blend freely, they are fresh typical centres or sub-species, which suddenly arise we do not yet know precisely through what uncommon concurrences of circumstance, and which observations show to be strongly transmissible by inheritance

A mere variety can never afford a sticking point in the forward course of evolution, but each new sport implies a new condition of internal equilibrium, and does afford one A change of type is effected, as I conceive, by a succession of sports or small changes of typical centre, each being in its turn favoured and established by natural selection to the exclusion of its competitors The distinction between a mere variety and a sport is real and fundamental I argued this point in a recent work ('Natural Inheritance,' Chapter III., MACMILLAN, 1889), but had then to draw my illustrations from non-physiological experiences I could not at that time find an appropriate physiological one The want is now excellently supplied by observations of the patterns made by the papillary ridges on the thumbs and fingers



## II *Observations on the Anatomy and Development of Apteryx.*

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[PLATES 3-19.]

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## I—INTRODUCTORY

THE chief materials for the present investigation consist of a number of embryos of the three common species of *Apteryx* which have come into my possession during the last three or four years. For some time I only succeeded in obtaining two or three specimens of advanced stages, and it was only when I was fortunate enough to secure the services of Mr RICHARD HENRY, of Lake Te Anau, as collector, that my material became copious enough to be worth working up. Even now my observations are in many respects very imperfect owing to the lack of a sufficient number of specimens, many of the most important stages being represented only by a single embryo.

Since communicating a preliminary note (28)\* on the subject to the Royal Society I have found it necessary to extend my investigations, so as to include certain points in the structure of the adult, especially the pterylosis and the characters of the wing, the sternum, shoulder-girdle, and skeleton of the fore-limb, the muscles of the wing, and the brain.

I beg to return my sincere thanks to the Council of the Royal Society for the grant from which the expenses of the investigation were defrayed, to Madame MULLER, for a half ripe embryo of *Apteryx oweni*; to Sir WALTER BULLER, for two advanced embryos of *A. bulleri*, to Professor HUTTON, for a wing of the rare *A. haastii*, to Sir JAMES HECTOR, for two skeletons, and for the opportunity of examining the collections in the Colonial Museum, Wellington, to Mr. H. O. FORBES, for similar facilities enjoyed at the Canterbury Museum, Christchurch, and for a skeleton of *A. oweni*, in a very interesting stage of development, to Mr T. W. KIRK, for valuable help during my work at the Wellington Museum; to Mr. T. F. CHEESEMAN, for two living specimens of *A. bulleri*; to Professor MAX FURBRINGER, for a copy of his magnificent work on the anatomy and classification of Birds; to my colleague, Dr. J. H. SCOTT, for valuable help in connection with the literature of the subject; and to my pupil, Mr. J. M. BEATTIE, for working out the percentages in Table B, p. 41.

\* The figures in brackets refer to the bibliographical list at the end of this paper (p. 117)

It is only right to state that my obligations to my collector, Mr HENRY, are out of all proportion to the sums paid to him for specimens. It has been of great advantage to me in many stages of the enquiry to have the opportunity of corresponding with so excellent a field-naturalist.

Perhaps I may also be allowed to mention that I have enjoyed the privilege of frequent correspondence with my Father on the subject-matter of my work. My chief hope in connection with the present paper is that it may be deemed worthy to serve as a supplement to the long series of researches on the anatomy of birds to which so many years of his life have been devoted.

## II—GENERAL DESCRIPTION OF THE STAGES EXAMINED

The embryos hitherto obtained naturally group themselves into ten stages (A to K). An eleventh stage (L) is furnished by a bird a few weeks old, a twelfth (M) by the skeleton of an adolescent specimen, and a thirteenth (N) and fourteenth (O) by odd bones of young birds. The adult may be considered as constituting a fifteenth stage.

The following table gives a list of the specimens examined —

Stage	Number of Specimens			
	<i>A. bulleri</i> *	<i>A. australis</i>	<i>A. owenii</i>	
A		1	.	} Embryos
B		1		
C		1		
D			1	
E			1	
F			1	
G		1	1	
H	1		1	} Time of hatching Several weeks old Skeleton of young specimen Skull and pelvis only of young specimen Loose bones of young specimen Entire specimens Skeletons
I	1	2		
K	1	2		
L		1		
M		.	1	
N		.	1	
O			1	
Adult {	2†	1	.	
	1	3	3	

In addition to these I have examined several wings taken from stuffed specimens or skins, and two skeletons the species of which are uncertain. One, in the Wellington Museum, was prepared by the late Dr. F. J. KNOX, who named it

\* This species is better known as *A. mantelli*, but Mr SHARPE has unfortunately, although no doubt correctly, found it necessary to change its name.

† Both these specimens had to be stuffed, so that only certain parts were available for examination.

*A maxima*. It appears to be a sub-adult *A bulleri*. The other I have provisionally referred to *A haastii* for reasons given hereafter (p. 39).

The chief gaps are between stages C and D and between stages G and H. With these exceptions, the series is fairly complete.

All the embryos were preserved in alcohol. As they had to be removed from the egg by the collector, the employment of special fixing reagents was inadmissible. They were for the most part well preserved, but not sufficiently well for the purposes of exact histological study. For sectioning they were stained *in toto* with borax-carmin, and imbedded in paraffin, serial sections being cut with the Thoma-Jung microtome. MEYER'S albumen and glycerine fixative was used. In most cases the sections were cut to a thickness of about  $\frac{1}{40}$  to  $\frac{1}{70}$  mm.

The embryos were drawn as a whole before cutting, the smaller ones (stages A-C) both as opaque objects and after being rendered transparent by turpentine. All microscopic drawings were made by the aid of ABBE'S camera lucida.

#### *Stage A* (Plate 3, fig. 1).

The single embryo belonging to this stage corresponds in most respects to a chick of the fourth day.\*

The body is so bent upon itself that the posterior cephalic and thoracic regions are approximately parallel to one another, and the end of the curved tail is almost in contact with the top of the head. The cerebral flexure is well marked, the angle between the fore and hind brain being acute. (*Cf* fig. 17, Plate 4.) The total length of the embryo, measured along the curve of the back from the nostril to the end of the tail, is about 20 mm. In its naturally curved condition it is about 6 mm. across.

The lateral curvature of the body is very much less than in the corresponding stage of the Chick. In the latter, at about the fourth day, a sagittal section of the whole embryo cuts the notochord, mesoblastic somites, myelon, &c., in very various planes. In the present instance nearly the whole of the notochord, except its caudal portion, was displayed in a single section.

The number of mesoblastic somites was difficult to count in the entire embryo, as it was not examined fresh, but by examining in turpentine by transmitted light it could be made out with tolerable certainty to be about forty-four—certainly not fewer than forty-three, nor more than forty-five. That is to say, the total number of segments is already acquired, since the number of vertebræ in the adult skeleton is about forty-five.

The limbs are in a far less advanced condition than in FOSTER and BALFOUR'S figure of the fourth day Chick (10, fig. 67). Each (fig. 1) has the form of a flattened,

\* I have unfortunately no good series of figures of the external form of chick-embryos which could be taken as a standard of comparison. The embryos I have myself obtained differ considerably in point of development from the corresponding ages as described by FOSTER and BALFOUR.

almost semicircular bud, the hind (*HL*) being already slightly larger than the fore limb (*FL*)

The position of the limbs at this early stage is apparently somewhat unusual. The fore-limb springs from the Wolffian ridge over against the seventeenth to the nineteenth mesoblastic somites (see fig 1, where the sixteenth somite is marked *mes som 16*), the hind limb over against the twenty-eighth to the thirty-sixth. In the Chick, according to FOSTER and BALFOUR's figure, the fore-limb, at a corresponding or slightly later stage, is opposite the tenth to the thirteenth somites, the hind-limb opposite the twenty-third to the twenty-sixth, the total number of somites being forty, or only four fewer than in the present stage of *Apteryx*.

In the adult both of *Apteryx* and *Gallus* the fore-limb lies in the transverse plane of about the sixteenth or seventeenth vertebra, the hind-limb in that of about the thirtieth or thirty-second. Thus while in *Gallus* the limbs undergo, subsequently to the fourth day, a backward shifting equal to the length of about six to eight mesoblastic somites, in an *Apteryx* of the corresponding age the adult position is already attained.

The ontogenetic shifting of the limbs of birds is very generally taken as evidence of a corresponding phylogenetic shifting. If this conclusion is correct—and there seems no reason to doubt it—the fact just described would seem to show that the interval separating *Apteryx* from its hypothetical short-necked ancestor is a wider one than has intervened in the case of *Gallus*. It must be remembered, however, that, according to FURBRINGER (11, p. 977), a forward displacement of the limbs occasionally occurs instead of the usual backward displacement, especially in the case of species with degenerating wings.

The first two visceral folds (mandibular, *Mn*, and hyoid, *Hy*) are considerably larger than the third, fourth, and fifth (figs. 19–21, *Br*, 1, 2, and 3). The superior maxillary process was not visible externally, nor can any trace of it be seen in sections, in this respect the resemblance is closer to a Chick of the third than to one of the fourth day (compare 10, figs 56 and 67).

In the brain the mesencephal (figs 1 and 17, *Mesen*) is proportionally smaller than in the Chick in correspondence with the relatively smaller eyes. The auditory sac (*Au*) has the usual characters, but the nasal sac (*Na*) agrees in character and position with that of a Chick of the third day, there is no trace of the fronto-nasal process and no overlapping of the nostrils by the lateral projection of the eyes.

The diameter of the allantois (*All*) was about five-sixths of the length of the head, i.e., of much the same relative size as in a Chick of the fourth day.

The embryo was cut into a complete series of sagittal sections.

### *Stage B* (Plate 3, fig 2).

This embryo is apparently only a few hours older than that just described, being considerably less advanced than a Chick of the fifth day. Measured across the curve



its length is about 7.2 mm, if straightened out it would measure, from nostril to end of tail, about 24 mm

The fronto-nasal process has barely begun to form, and there is still no trace of the superior maxillary process. The distinction between the mandibular and hyoid folds is less clear than in the previous stage, owing to the partial obliteration of the furrow between them. In the sections the post-hyoidean clefts (*Cl* 2) are seen to meet in the middle ventral line (fig. 28), and the hyoidean folds are slightly produced backwards, forming an operculum-like flap (figs 2, 28, and 29, *Operc*) over the neck, beneath which there is a transverse crescentic slit (figs 28 and 29, *Cl* 1), placing the pharynx in free communication with the exterior. I have no recollection of seeing this condition of things described in any vertebrate embryo, and am disposed to attribute it to an injury, although it is rather difficult to account for the destruction of the delicate median isthmus between the ventral ends of the hyoidean and first branchial folds, placed as it is in a very inaccessible situation, without any corresponding injury to the folds themselves. The third visceral cleft (*Cl* 3) is still open, but considerably reduced in size, the fourth (*Cl* 4) is closed.

The allantois (*All*) is now, as shown by the dotted outline, considerably larger than the head. In other respects there is very little advance.

Sections of this embryo were made parallel to the long axis of the head, with the result of getting longitudinal sections of the anterior cephalic (figs 22–24), cervical (fig 33) and middle caudal regions, and transverse sections of the posterior cephalic (figs 26–31), thoracico-lumbar (figs 31 and 32), and posterior caudal (fig 32) regions.

#### *Stage C* (Plate 3, figs. 3 and 4)

In this embryo, which corresponds in general features with a Chick of about the sixth day, there is a considerable alteration in form, accompanied by a slight increase in size. The total length from nostril to end of tail, measured along the curve of the back, is now about 30 mm., the greatest length across the curve about 8 mm.

As compared with the previous stages, there is a slight diminution of the cranial flexure, the general axis of the head being now as nearly as possible at right angles to that of the neck.

The fronto-nasal process (figs 3, 4, 35, and 36, *Fr Na.P*) has appeared as a prominent distinctly bilobed elevation, and the nasal sac (*Na.*) has, in consequence, become more deeply set, so as to have the appearance, externally, of a longitudinal slit, and not of an open pit. The superior maxillary process (figs. 3, 4, and 37) is also well developed, but runs much more nearly parallel to the mandibular arch (*Mn.*) than in the Chick.

The first visceral (mandibulo-hyoid) cleft (figs 3, 4, and 39, *Cl* 1) has the usual relation, the second, or post-hyoidean clefts (figs. 3, 4, 40, 41, and 42, *Cl* 2) have a great vertical extent, and nearly meet with one another in the middle ventral line.

(fig 40) The backward extension of the hyoidean fold visible in the previous stages has increased so as to form a true operculum (figs 3, 4, 41, and 42, *Operc*), which completely covers the third cleft (fig 42, *Cl* 3), so that it is invisible in an external view. The fourth cleft lies immediately behind the operculum, and is very probably only exposed by the shrinking of the latter as in the previous stage it no longer communicates with the exterior.

The retention of so obviously amphibian a character as the opercular fold in the embryo of *Apteryx* appears to be a character of very considerable morphological interest. I have not met with any record of its occurrence in other *Sauropsida*.

The limbs are no longer mere semicircular buds, but have become elongated and flattened dorso-ventrally, and their distal ends are slightly dilated. The disparity in size between the two pairs of limbs is now very obvious, the rudiment of the wing (*FL*) being hardly more than a third the size of that of the leg (*HL*).

The specimen was sectioned in the same direction as the last (*cf* Plate 5).

#### *Stage D* (Plate 3, fig 5)

This embryo was unfortunately much damaged by the collector during removal from the egg. The head was severed from the body, the surface was considerably abraded, and, worst of all, both fore-limbs were destroyed. Measured along the curve of the back it is about 43 mm from the end of the beak to the end of the tail.

The advance beyond the preceding stage is very marked, avian characters being definitely assumed. The general features correspond fairly with those of an eighth day Chick.

The head is rounded in side view, compressed laterally (Plate 9, figs 88–92), and produced into a short beak, slightly curved at the tip. Owing to the damaged state of the specimen, I could not be perfectly sure of the position of the nostril, but from a careful examination of the entire embryo, and afterwards of the transverse sections into which it was cut, I feel tolerably certain that it was situated as in fig 5 (*Na.*), that is, about half way between the base and the tip of the beak.

The visceral clefts have disappeared, with the exception of the first (*Cl* 1), which now forms the tympano-eustachian passage, and appears externally in its usual position below and behind the eye.

The neck is long and the tail very distinct. The fore-limb, as already mentioned, was destroyed on both sides. I have indicated its position and probable form by a dotted outline (*FL*). The hind-limb retains its embryonic position at right angles to the long axis of the trunk, and with its ventral or flexor surface directed mesiad. There is no flexure at either knee or ankle, but the pes is marked out by being broader and flatter than the rest of the limb, and produced dorsally into low ridges, indicating the position of the three principal digits (2, 3, 4). The hallux (1) is an inconspicuous projection on the preaxial border of the foot.

The specimen was cut into a complete series of transverse sections, the head, neck,

and trunk being cut separately. Of the hind limbs horizontal sections were taken, *i.e.*, sections parallel to the plane of the digits

*Stage E* (Plate 3, figs 6 and 7).

This very interesting stage is, like the last, represented by a single specimen a good deal damaged during removal from the egg. The head was severed, and the whole surface abraded. The total length is nearly the same as in the last stage.

The trunk has become straighter, but the tail is still large and curved. The head is rounded, and the beak proportionally longer than in the previous stage. The tip of the beak was damaged, so that the position of the nostrils was not apparent in the entire embryo, but sections showed their position to be as indicated in the figure (*Na*), namely, at the extremity of the beak. Thus the unique position of the external nares in *Apteryx* is established at a comparatively early stage of development.

In the eye the rudiments of the sclerotic plates are obvious, and the opening of the lacrymal canal is visible as a small pit immediately in front of the eye.

The fore-limb is bent at the elbow at a right angle. The manus is a tridactyle paw, being produced distally into three blunt projections, of which the middle one (2) is the largest, while of the other two the third (3), or postaxial, is slightly longer than the first (1), or preaxial, digit.

The hind-limb has also undergone a right-angled flexure at the knee, and at the same time the femur has rotated so that the combined crus and pes—which are still in the same straight line—are directed backwards, having their preaxial border mesial, and their originally dorsal (outer) surface looking downwards and forwards. The muscles of the thigh have undergone a notable development, so that this region of the leg has already its permanent laterally compressed form. The pes is still short, but the second, third, and fourth digits (figs. 7, 2, 3, 4) are well marked out, they are still connected by membrane, so that the foot at this stage is distinctly webbed. The hallux (1) has the form of a short blunt projection on the preaxial border of the tarsal region.

In this embryo the brain was removed, and the base of the skull drawn from above. The head was then imbedded, and sagittal sections of the left side cut until the mesial plane was reached, when it was turned, and the right half cut into transverse sections. The pectoral and pelvic girdles of one side were exposed, sketched *in situ* and removed, and a complete series of sagittal sections was then made of the trunk. The fore-limbs were then cut horizontally, *i.e.*, parallel to the plane of the digits, one of the hind-limbs horizontally, the other sagittally, *i.e.*, at right angles to the plane of the digits.

*Stage F* (Plate 3, figs 8 and 9).

This stage is of great interest as being the first in which the generic characters are fairly assumed; the long beak with its slightly curved tip, and sub-terminal nostrils

(*Nα*), mark the embryo at once as referable to no other genus than *Apteryx*. From the fact that, as shown by sections, ossification is just about to commence in the larger bones of the limbs and the membrane bones of the skull, the stage may be taken to correspond with a Chick of the eighth or ninth day. The entire length from tip of beak to end of tail is now about 60 mm. The head has attained its maximum relative size.

The form of the head, apart from the beak, and the form and curvature of the trunk, are much the same as in the previous stage, but the tail is relatively smaller, and so are the eyes.

The fore-limb is now an undoubted wing, the second digit (fig. 9, 2) has grown out of all proportion to the first (1) and third (3), which form mere blunt projections on the pre- and post-axial borders respectively.

In the hind-limb the thigh is, as in the adult, hardly distinguishable from the outside, the knee only just appearing beyond the general contour of the body. The mesotarsal flexure has appeared, and the toes are directed ventrad. The tarsal region has elongated considerably, the digits are quite free from one another, and have an almost regularly cylindrical form. There is still no trace of claws. The hallux (1) has undergone a considerable shifting distad, its adult position being nearly attained.

The first rudiments of the feather-papillæ are visible. There is a well-marked dorsal tract (*Dors Pt*) extending from the occipital region to the rump, it occupies about the dorsal half of the circumference of both neck and trunk, and divides at the root of the tail-papilla, which is itself quite bare. The dorsal pteryla is continuous on each side with a weak and inconspicuous femoral tract (*Fem. Pt*), and there is a small but well-marked humeral tract (*Hum Pt*).

A dissection of this embryo was made from the left side, and the skull with the brain, the pectoral and pelvic girdles, and the ribs and sternum, were sketched *in situ*. The head was then disarticulated, the brain removed, and the base of the skull drawn from above and from below, a model of the brain-case was also made in clay. The head was then stained and embedded, and, as in the previous stage, sagittal sections of the left half and transverse sections of the right half were cut. The shoulder and hip girdles and the sternum and ribs of one side were removed and mounted separately, and the trunk then cut into sagittal sections. The wings were sectioned horizontally, while of the legs one was cut into horizontal, the other into sagittal sections.

#### *Stage G* (Plate 3, figs. 10 and 11)

One of the two embryos belonging to this stage (*A. owenii*) was found to be crushed quite flat from side to side, apparently by the weight of the superincumbent yolk, the egg having been opened and placed entire in alcohol. The following description applies, therefore, to the specimen of *A. australis*.

From the fact that the shafts of the principal long bones of the leg and the

membrane bones of the skull have begun to ossify, this stage may be taken to correspond with a Chick of about the eleventh or twelfth day.

The total length from the tip of the beak to the uropygial papilla is about 90 mm. The form of the head has undergone but little alteration, but the relative length of the beak has increased considerably. Owing to the development of the eyelids the eyes appear much smaller than in the previous stage, the sclerotic plates being completely hidden, as well as the opening of the lacrymal duct. The nictitating membrane has appeared.

The tail is reduced to a small rounded uropygium (figs 10 and 11, *Upg*), immediately cephalad of which is a rounded area having its margin depressed below the general level of the region, and devoid of feather papillæ. This area, which is subsequently modified into the lips of the cloaca, has near its anterior margin a deep depression, from which springs a prominent papilla, bearing the cloacal aperture (*Clo ap.*), towards the posterior (caudal) aspect of its summit.

The wing is relatively slightly smaller than in the previous stage, and has assumed quite the adult form, there being no trace externally of either the first or the third digit.

The legs have undergone a great increase in size, the digits have lengthened very considerably, and each is now tipped by the rudiment of the horny claw, at the base of which is an annular fold of skin.

The feather papillæ are now very prominent, especially on the rump. A distinct tract has appeared on the dorsal surface of the head, and another on the ventral aspect of the neck extending a short distance on to the pectoral region, and becoming confluent with the humeral tracts (*Hum Pt*).

A complete series of transverse sections was made of the head, neck, and trunk of the specimen of *A. australis*, as well as horizontal sections of the wings and feet. In *A. owen* the skeleton was prepared by dissection.

#### *Stages H-K* (Plate 3, figs. 12 and 13)

From Stage H onwards the embryo has practically acquired all the adult characters, except that the feathers are hair-like, the barbs being still enclosed in a sheath of the stratum corneum.

Fig 12 shows an embryo of Stage I after removal of the feathers. The dorsal and ventral tracts so distinct in Stage G, have met and coalesced on the sides of the neck, but on the trunk the lateral apterium (*Lat Apt.*) is quite distinct, extending from the region of the wing backwards on to the rump. There is also a well-marked ventral space (*Vent. Apt*), and the whole inner (ventral) aspect of the wing is devoid of feathers, forming an inferior alar apterium (fig. 13, *Inf. Al. Apt.*). The remiges are no larger than the contour feathers, and as in all other stages the uropygium (*Upg.*) is naked, presenting no feathers round its base which can be identified as rectrices.

As compared with the previous stages the relative diminution in size of the head,

the elongation of the beak, and the immense increase in all dimensions of the legs, are particularly noticeable

My observations on these stages, as well as on many of the previous ones, relate exclusively to the skeleton and the brain. Most points were made out by dissection, but verification by serial section was constantly resorted to, the wings of several specimens being examined in this way, as well as the entire head of an example of *A. owenii* belonging to Stage H.

Neither in these nor in any of the previous stages was there any trace of the little rounded caruncle, or "egg-breaker," on the end of the beak, which is so marked a feature in most Carinate Birds. My Father tells me that he knows of no other bird in which it is absent, I have myself observed it in Gulls, Petrels, Ducks, and Penguins, but there is no trace of it in the advanced embryo of a Dottrel (*Charadrius bicinctus*?) in my possession. It is not indicated in Miss LINDSAY's figures of Ostrich embryos (19, Plate 43), and, according to ROLLESTON and HATCHETT JACKSON (48, p. 379), it is not always present.

### III—REMARKS ON THE EXTERNAL CHARACTERS OF THE ADULT

It is constantly stated in zoological works that the Ratitæ are distinguished by an uninterrupted pterylosis. NITSCH says (23, p. 118) that "the whole body, with the exception of the constantly naked parts of the head and neck, the naked band on the breast along the crest of the sternum, the tarsi, and, in the African Ostrich, the legs and the sides of the trunk, is covered, after the fashion of Mammals, with a homogeneous feathery coat." This statement is practically repeated by FURBRINGER (11, p. 1010) and by WIEDERSHEIM (52, p. 31), to mention only two important modern works which deal with the question. Pterylæ and apteria are, however, shown in Miss LINDSAY's figures of Ostrich embryos (19, Plate 43), but they are only briefly referred to in the explanation of the plate.

In the adult *Apteryx*, as in advanced embryos, the pterylosis is by no means uninterrupted. In a fresh specimen of *A. bulleri* I find the lateral apterium to be fully 2 cm. wide, and to extend about 5 cm. cephalad and 9 cm. caudad from the axilla, its total length being therefore about 14 cm. In the same specimen, the ventral or inferior space was of about equal width (2 cm.), and extended about 11 or 12 cm. caudad from between the origins of the wings. Moreover, the inner (ventral) surface of the wing is always nearly devoid of feathers (Plate 3, fig. 15), and so constitutes a well-marked lower wing-space.

According to NITSCH, the function of the lateral apteria "seems to be, not only the facilitation of the movements of the wing, but likewise to serve for the reception of the folded wing, in such a manner that it may be supported upon the feathers of the branch of the ventral tract." It seems reasonable, on this view, to suppose that the



presence of a large lateral space is evidence of the wings having been larger in the ancestors of the Kiwi than in the existing genus.

I find, however, that the space in question has a definite function in connection with the attitude assumed by the bird during sleep. According to POTTS (46), "the mode of roosting is very peculiar, they squat opposite each other with their legs bent under them, each with its head tucked under the scanty apology for a wing." Careful observation of living specimens of both *A. australis* and *A. bulleri* shows that this statement is not quite correct. When a Kiwi is settling down to sleep it squats as described, resting upon the whole length of the foot, the rump being in contact with the ground, and the trunk at an angle of about 45°. The head, after a little preliminary fidgetting, is then turned round to the right, and the beak gradually worked under the side feathers, apparently until the lateral apterium is found by its sensitive tip—it is then somewhat quickly thrust backwards beneath the feathers—the action resembling that of sheathing a sword—until it is completely hidden. On carefully turning the feathers aside without disturbing the bird, it was found that the beak was placed along the lateral apterium, with its base immediately cephalad of the axilla. As the wing is so placed in the position of rest that the upper arm is directed from the axilla upwards and backwards, the base of the beak lay in a kind of trough, bounded mesiad by the trunk and laterad by the wing, the naked elbow being very obvious as a small flesh-coloured projection just external to it. In this position the distal portion of the wing is thrust somewhat outwards, and its feathers—remiges and upper coverts—appear externally, taking a direction downwards and backwards over the ordinary contour feathers of the trunk.

It is rather significant that this is precisely the attitude of a Goldfinch or Canary when asleep, the beak in these cases being over (dorsad of) the axilla and therefore, of course, under the spreading side feathers. Perhaps the facts may be explained by supposing that during the evolution of the genus *Apteryx*, the great lateral spaces were retained as resting places for the increasing beak, although no longer useful for the reception of the diminishing wings.

Another fact which appears to me to tell in favour of the derivation of *Apteryx* from a progenitor with well developed wings, is the fact that the wing is provided with a true alar membrane. Both OWEN's figure (24, Plate 1, fig. 4), which shows the wing of *A. australis* from the outer side with most of the feathers removed, and BULLER's (7, Plate 12, fig. 6), which shows that of *A. bulleri* from the inner side with the feathers *in situ*, are apparently taken from somewhat shrivelled specimens. The wing of a perfectly fresh specimen of *A. bulleri* is shown in figs. 14 and 15 (Plate 3). It has, precisely as in typical Carinatae, a distinct fold of skin, or pre-patagium, passing between the upper arm and fore arm, as well as an equally well marked fold, the post-patagium, between the postaxial border of the upper arm and the trunk.

The characters of the alar claw do not appear to have been described with any accuracy, and are of some interest as seeming to furnish a very fair specific character.

As far as my experience goes, the alar claw of *A. oweni* is always soft and weak, gently curved, about 4 mm. long, and of a light horn colour (Plate 17, fig 243). That of *A. haastii* is quite similar, but sometimes even smaller the left claw of the supposed female specimen in the Canterbury Museum being only 3 mm long, in the supposed male, Professor HUTTON informs me it is about 9 mm long, much curved and white. In *A. australis* it is about 6–8 mm long, gently curved, and of a light horn colour, blotched with black (fig 241). Lastly, in *A. bulleri*, it is strongly curved, from 6 to 18 mm long, and quite black (figs 245 and 246). It seems to be constantly larger in the male than in the female, and often differs on the two sides of the body.

As to the form and arrangement of the wing feathers, YARRELL (55) in the earliest accurate description of *Apteryx*, states that these do not differ from the feathers of the body generally, and apparently OWEN (24, p. 3) was the first to point out the presence of remiges, he says "nine quasi-quill-plumes, not exceeding in length the ordinary body feathers, but with somewhat thicker shafts, are arranged in a linear series along the ulnar margin of the antebrachium." FLOWER's observations referred to by WRAY (54) are not mentioned in the abstract of his lecture on the Wings of Birds (9), but in answer to my enquiries, Professor FLOWER was good enough to inform me that he had found eight cubitals and one metacarpo-digital in the specimen of *A. oweni* mounted for the British Museum, but that several feathers of both sets appeared to be wanting as the bird was moulting.

According to my own observations, made chiefly upon two fresh specimens of *A. bulleri*, and confirmed upon examples of the other three species, there are nine or ten cubitals (figs 14 and 15 *Cubit*), of which the five distal (Nos. 1–5) are larger than the rest, two or three metacarpals (*Met*), and a single mid-digital (*Mid dig*), the latter being usually smaller than the rest. The formula for the remiges is therefore

$$Md\ 3-4\ (m\ 2-3,\ d\ 1),\ C\ 9-10$$

On the outer side of the wing there is a row of well-marked tectrices majores (fig. 14, *Tect. maj.*), which correspond accurately with the remiges in the distal portion of the series, but towards the proximal end of the row of cubitals become more or less irregularly arranged. The remaining upper coverts are not definitely disposed in rows, so that there is no distinction between tectrices mediæ, tectrices minores, and marginals. The few feathers on the under or inner side of the wing are all directed proximad or towards the axilla (fig. 15), not distad like the upper coverts.

In microscopic structure the feathers agree with those of *Rhea* as described by FURBRINGER (11, p. 1482). The barbules (Plate 3, fig 16) are beset with regularly arranged pointed barbicels slightly curved outwards at their tips, and, as far as my observations go, larger in the unhatched embryo than in the adult.

On the whole it appears to me that the structure of the wing of *Apteryx* lends support to the view that the Ratitæ are the descendants of Birds which possessed the power of flight, a view which, I believe, OWEN was the first to advance. In spite of



Miss LINDSAY's conclusions from her study of the development of the sternum (19), and WRAY's from his researches on the wing (54), I am still disposed to think that the balance of evidence is in favour of the hypothesis to which I was led by a study of the flightless Rallidæ (26), that the Ratitæ spring from a proto-carinate stock, a theory which has recently received strong support from the researches of FURBRINGER (11) and of GADOW (13)

It has always seemed to me that, on the hypothesis of its development from an ordinary Reptilian fore-limb, *e.g.*, that of a Dinosaur, the wing is one of the most striking examples of the uselessness of incipient structures. If, on the other hand, we suppose it to have been evolved from a patagium which gradually diminished *pari passu* with the development of its scales into feathers, the difficulty of its first origin is overcome and the presence of the alar membranes is explained.

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#### IV—THE LAW OF GROWTH

(Plates 6 and 7)

A very interesting mode of comparison of aberrant—either highly specialised or highly generalised—forms with their more typical congeners, is furnished by observation of the relative rate of growth of various regions of the body from an early stage of development to adult life. The difference between the law of growth of Man and of the other Primates is an example which will occur to everyone. I think it will be useful to furnish materials towards an enquiry into the general law of growth in Birds by giving a series of measurements of the various stages of *Apteryx*, as is done in Table A. In the adult it will be seen that measurements of both sexes are given in the case of *A. australis* and *A. owenii* of *A. bulleri* I have been able to measure only a single skeleton. This is, however, of comparatively little importance since *A. australis* and *A. bulleri* agree with one another so closely in size and proportions. Moreover, as already stated (p. 28) the so-called *A. maxima*, of which measurements are given, is probably referable to this species.

Measurements are also given of a skeleton which I have named doubtfully *A. haastii*, a species which was founded by PORTS (45) upon two skins from the west coast of the South Island and now in the Canterbury Museum. By the kindness of Professor HUTTON, at that time acting Director of the Museum, I was enabled to examine the wing of one—the supposed female—of the type specimens, and found it to differ from all examples of *A. australis* (which it resembles in size) and to agree with *A. owenii* in the possession of a distinct radiale in the carpus (see p. 93, and Plate 17, fig. 250), and in the characters of the alar claw (p. 37).

The doubtful skeleton referred to was obtained near Cape Providence, on the west coast of the South Island, in 1881, by a collector named WHEELER, who left it in the landing shed of the Puysegur Point Lighthouse before starting for another expedition

TABLE A —Measurements of Developmental Stages of *Apteryx* in millimetres

Stage	A	B	C	D	E	F	G	H	I	K	L	M	Adult A bulleri, ♀	Adult A maxima = bulleri	Adult A australis, ♂	Adult A australis, ♀	Adult A haastii, ♀	Adult A owen, ♂	Adult A owen, ♀
<i>Vertebral column</i> , length, following the curve	9	10.5	13	19	21	27.5	44	90	120	172	200	255	396	400	380	445	430	288	320
<i>Brain-case</i> , length in a straight line from occiput to base of beak (descending process of nasal)		..		7.2	7	9	12	20	23	29	32	35	43	45	46	49	48	34	36
<i>Beak</i> , length from base (descending process of nasal) to tip				2.2	2.5	7	12	28	35	49	60	72	140	125	114	146	118	79	84
<i>Entire head</i> , from occiput to tip of beak	3	3.7	4.2	8.7	9	15.5	24	48	58	78	92	107	183	174	160	195	160	113	120
<i>Sternum</i> , greatest length in a straight line				?	1	3.5	3.75	11	15	23	26	27	38	39	42	45	49	28	30
<i>Coracoid</i> ditto				?	1.2	1.6	2	3	4.5	8	9	11	17	18	17	20	20	13	14
<i>Scapula</i> ditto				?	1.5	2.4	3.5	8	11.5	17	19	24	27	25	28	28	30	25	27
<i>Entire shoulder girdle</i> ditto ditto		.		?	2.7	4	5.5	11	16	25	26	32	42	43	42	46	46	35	36
<i>Humerus</i> ditto				?	1.5	3	4.75	9.5	14	21	25	31	43	43	44	48	47	34	36
<i>Antebrachium</i> ditto				?	0.9	1.5	2.8	5	7	12	13	17	24	23	23	25	21	15	17
<i>Manus</i> ditto				?	1.1	1.5	1.5	3	5	7.5	10	10	12	14	15	14	13	10	11
<i>Entire fore-limb</i> ditto ditto	0.25	0.5	0.6	?	3.5	6	9.1	17.5	26	40.5	48	58	79	80	82	87	81	59	64
<i>Ilium</i> ditto				3.2	4	7	9.75	23	30	44	50	72	101	113	112	123	123	76	81
<i>Femur</i> ditto				2.5	4	6	7.5	19.5	26	42.5	50	69	99	92	96	107	104	72	76
<i>Crus</i> (to mesotarsal joint), in a straight line				3	4	7.5	11	27	37	61.5	70	94	134	136	140	145	148	101	101
<i>Tarso-metatarsus</i> , greatest length in a straight line	.			1.4	2.2	3.5	7	16	23	38	43	49	71	75	72	76	76	51	55
<i>Middle (third) digit</i> ditto ditto	.	.		0.7	1	2	5	16	22	38	43	45	62	65	68	66	68	50	50
<i>Entire pes</i> , from mesotarsal joint to end of third digit				2.1	3.2	5.5	12	32	45	76	86	94	133	140	140	142	144	101	108
<i>Entire hind-limb</i> , greatest length	0.4	1	2.5	7.6	11.2	19	30.5	78.5	108	180	206	257	366	368	376	391	396	274	288

\* See p 28

from which he never returned. The skeleton was found by the lighthouse keeper, Mr. J. W. CUNNINGHAM, and given to my taxidermist, Mr. E. JENNINGS, to whom I am indebted for the opportunity of examining it. It presents the following peculiarities—It is as large as an average female *A. australis*, but the beak is little longer than in the male of that species and proportionally no longer than that of *A. oweni* (see Table B). The left manus has a distinct radiale (Plate 17, fig. 251), and the alar claw, which was present on both sides, is small and light coloured, as in *A. haastii* and *A. oweni*. The sternum also (Plate 16, fig. 210) is unusually long. These characters by no means prove the skeleton in question to be anything more than a somewhat aberrant example of *A. australis*, but they are enough to warrant separate measurements being given.

In addition to the Table (A) of actual measurements, another (B) is given in which comparison is facilitated by taking the length of the vertebral column as = 100 and expressing the remaining measurements as percentages. It is only by using some such method as this that the changes of proportion of various parts of the body during the course of development can be clearly shown. In comparing *Notornis* with other Rails (26) I took as my standard the length of the trunk as measured from the anterior end of the coracoid to the posterior end of the pelvis; FURBRINGER (11) employs for the same purpose the length of a thoracic vertebra. But both these methods would preclude the comparison of the earlier stages, and on the whole I am disposed to think that the standard here adopted answers the purpose satisfactorily. Graphic representations of the same facts are given in Plates 6 and 7. In fig. 45 the various parts of the body are represented in a conventional manner, the vertebral column being made in each case 100 mm long, and the head, limbs, etc., in proportion. In figs. 46-49 the curves of growth of certain important regions are shown separately.

The following are the most important results obtained by this method of enquiry.

The brain-case remains of about the same relative size up to Stage F, when it begins to grow less rapidly than the vertebral column. The age at which its ultimate or minimum proportional size is attained is not known, but in a young bird several weeks old (Stage L) it was not yet reached.

The beak, which is undeveloped in the first three stages, is of about the same size in D and E, in F it has undergone a notable increase, in G it is of the same length as the brain-case, and its maximum proportional length is attained in H. It is worthy of remark that, as shown in Table B and fig. 46, the proportional length of the beak is nearly the same in the two sexes, although its absolute length is so much greater in the female; in *A. oweni*, indeed, the beak of the male was found to be relatively longer than that of the female, but this was very probably an individual variation.

The sternum (fig. 47) attains its maximum in Stage F, thereafter undergoing but little variation in relative size. It is important to note, however, that up to Stage G the postero-lateral processes are not formed (Plate 16, figs. 216-218), so that its

TABLE B—Measurements of *Apteryx* expressed as Percentages of Length of Vertebral Column

Stage	A	B	C	D	E	F	G	H	I	K	L	M	Adult A bulleri, ♀	Adult A australis, ♂	Adult A australis, ♀	Adult A haastii, ♀	Adult A owenii, ♂	Adult A owenii, ♀
<i>Vertebral column</i>	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
<i>Brain-case</i>		..		37 89	33 3	32 72	27 27	22 2	19 16	16 8	16	12 28	10 87	12 1	11 01	11 16	11 8	11 25
<i>Beak</i>		.	..	11 57	11 9	25 45	27 27	31 1	29 16	28 48	30	25 26	35 35	30	32 8	27 44	27 43	26 25
<i>Entire head</i>	33 3	35 23	32 3	45 78	42 85	56 36	54 55	53 3	48 3	45 34	46	37 54	46 21	42 1	43 82	38 6	39 23	37 5
<i>Sternum</i>				?	4 76	12 72	8 52	12 2	12 5	13 37	13	9 47	9 59	11 05	10 11	11 39	9 72	9 37
<i>Coracoid</i>			..	?	5 71	5 21	4 54	3 3	3 75	4 65	4 5	3 85	4 29	4 47	4 49	4 65	4 51	4 37
<i>Scapula</i>			.	?	7 14	8 72	7 95	8 8	9 58	9 88	9 5	8 42	6 81	7 36	6 29	6 97	8 65	8 43
<i>Entire shoulder girdle</i>	.			?	12 85	14 54	12 5	12 2	13 3	14 53	13	11 22	10 6	11 05	10 33	10 69	12 15	11 25
<i>Humerus</i>	..			?	7 14	10 9	10 79	10 5	11 6	12 2	12 5	10 87	10 85	11 57	10 78	10 93	11 8	11 25
<i>Antebrachium</i>				?	4 27	5 45	6 36	5 5	5 8	6 97	6 5	5 96	6 06	6 05	5 61	4 88	5 2	5 31
<i>Manus</i>	.	.		?	5 23	5 45	3 4	3 3	4 16	4 36	5	3 5	3 03	3 94	3 14	3 02	3 47	3 43
<i>Entire fore-limb</i>	2 7	4 76	4 61	?	16 6	21 81	20 69	19 4	21 6	23 54	24	10 35	19 94	21 57	19 55	18 8	20 48	20
<i>Ilium</i>	..		.	16 7	19 04	25 45	22 15	25 5	25	25 58	25	25 26	25 5	29 47	27 64	28 6	26 38	25 3
<i>Femur</i>	.			13 15	19 04	21 81	17 04	21 6	21 6	24 7	25	24 21	25	25 2	24 04	24 18	25	23 7
<i>Crus</i>	.			15 78	19 04	27 27	25	30	30 8	35 75	35	32 9	33 83	36 84	32 58	34 41	35 07	32 5
<i>Tarso-metatarsus</i>			.	7 36	10 47	12 72	15 9	17 7	19 1	22 09	21 5	17 19	17 92	18 9	17 09	17 67	17 7	18 12
<i>Middle (third) digit</i>				6 38	4 76	7 27	11 36	17 7	17 5	22 09	21 5	15 7	15 65	17 89	12 58	15 81	17 37	15 62
<i>Entire pes</i>				11 05	15 23	20	27 27	35 5	37 5	44 18	43	32 9	33 55	36 84	31 91	33 48	35 07	33 75
<i>Entire hind-limb</i>	4 4	9 52	19 23	40	53 3	69 09	69 31	87 2	90	104 65	103	90 17	92 37	98 93	88 53	92 09	95 13	90

\* See p 28

potential is very much greater than its actual length, and the comparison with later stages is hardly fair

The shoulder-girdle (fig 47) hardly changes in proportional size from the time it was first observed (Stage E). The coracoid is of much the same size in all species, but the scapula appears to be longest in *A. oweni*.

The pelvis (fig. 47) attains its maximum in Stage F, remaining about the same throughout life, save for what are probably individual variations, in *A. oweni*, but increasing slightly after hatching (Stage K) in *A. australis*. In all the skeletons examined the relative size of the pelvic girdle was slightly greater in the male than in the female.

The fore-limb (fig 48), taken as a whole, increases pretty regularly up to Stage F, and then remains stationary, subsequent variations being obviously individual. The variations in the two sexes and in the different species, in the adult, would probably disappear if the average of a sufficiently large series of specimens was taken. As to the separate divisions of the wing the only point worthy of mention is that in Stage E the manus is longer than the antebrachium, while in F the two are of the same length, and in G the adult proportions are attained.

The curve of growth of the hind-limb is very different (fig 49). The entire limb increases rapidly and with but slight fluctuations, due no doubt to the observations being made on single specimens, from 44 per cent. of the vertebral column in Stage A to 104.6 per cent. in Stage K. In the adult it varies from 88 per cent. (*A. australis*, ♀) to 98 per cent. (*A. australis*, ♂), thus undergoing a relative diminution in size between the time of hatching and the attainment of fully adult proportions. It is quite possible that this rather remarkable result is to be put down to individual variation, but I hardly think so, as the three specimens belonging to Stage K and the single specimen of Stage L (not shown in the diagram) all have the hind-limb more than 100 per cent. of the vertebral column, while in the adult it was below 95 per cent. in six out of seven skeletons measured.

The four divisions of the limb—femur, crus, tarso-metatarsus, and middle (third) digit—increase in much the same manner as the whole limb, the only point worthy of special mention being the fact that the middle digit is at first (Stages D and E) not more than half the length of the tarso-metatarsus, while from Stage E onwards it gradually increases until the two divisions of the foot are of equal length in H. This proportion is retained as far as L, but in the adult the middle digit is, in seven skeletons measured, slightly shorter than the tarso-metatarsus. So that in the relative proportions of the two divisions of the foot, as in that of the entire hind-limb, the maximum differentiation appears to be attained about the time of hatching, a retrogression towards more embryonic proportions taking place subsequently.

As to sexual and specific differences I find that the legs of the male are relatively longer than those of the female. In the skeletons examined the legs of the male are

proportionately longer in *A. australis* than in *A. owenii*, while in the female the reverse is the case. This, again, is very probably a matter of individual variation.

A brief statement of the law of growth in *Apteryx* is given in the Summary (p. 111).

## V—THE SKELETON

The detailed accounts of the skeleton of *Apteryx* by OWEN (24), BLANCHARD (6), and MIVART (21), render any full account of the general adult osteology quite superfluous. The observers referred to have, however, only had the opportunity of describing adult or sub-adult specimens. Their material has, moreover, consisted of a small number of examples, so that they have been unable to take account of the individual variations, some of which, as will be seen hereafter, are of considerable interest.

I propose, therefore, to begin my account of each portion of the skeleton by describing somewhat fully either the condition of the part in question in the ripe embryo, in which the various ossifications are distinct, or the adult structure in cases where, owing to paucity of material, the descriptions of former observers are imperfect.

I have found it convenient to add two new terms to the general terminology of the skeleton. An independent cartilaginous element or centre of chondrification is called a *chondrite*, an independent bony element or centre of ossification an *osterte*, both words being formed on the model of the well-known entomological term "sclerite."

### 1 THE SKULL

#### a. *At the Time of Hatching (Stage K).*

(Plates 8 and 9.)

OWEN's descriptions of the skull (24) are taken from a fully adult specimen of *A. australis*, and from one in which the frontal and left half of the coronal\* sutures were persistent. The skull of the same species figured by BLANCHARD (6) had the sagittal, coronal, and middle third of the lambdoidal sutures open, and many of the membrane bones were distinct, but the bones of the basis crani were united, and the turbinals do not appear to be shown.

In the skull of Kiwi chicks, either shortly before or shortly after hatching, all the ossifications have appeared, and the only ankyloses are those between the right and left premaxillæ, dentaries, and splenials, and between the basi- and para-sphenoids. After maceration the membrane bones are readily detached.

\* Both in OWEN's original monograph and in the reprint the coronal suture is, obviously by a printer's error, called sagittal.

Figures of the entire skull and of the separate membrane bones are given in Plate 8, figures of the chondrocranium in Plate 9. Sections through important regions in a somewhat earlier stage (H) are given in Plates 12-14, and will be occasionally referred to.

### *The Chondrocranium*

By the removal of all the membrane bones, except the already ankylosed parasphenoid (basitemporal *plus* rostrum) the chondrocranium (Plate 9, figs. 75-77) is obtained as a basin-shaped mass of mingled bone and cartilage, produced in front into the elongated olfactory capsules (fig. 75, *Ec Eth*) and prenasal rostrum (*Pr Na*). The short basis crani (*B Oc*, *B Sph*) is continued behind into the occipital arch (*S Oc*), and on each side into the auditory capsules (*Pr Ot*), and alisphenoids (*Al Sph.*), while in front it bears the deep, transversely elongated, pituitary fossa (*Pty F.*)

All the cartilage bones of the fully developed cranium have appeared, and, with the exception of the isolated ethmo-presphenoid bone (*Eth Pr.Sph*), are separated from one another by narrow synchondroses.

The *basioccipital* (*B Oc*) is roughly pentagonal in form, and bears posteriorly the transversely ovoid occipital condyle (*Oc Cn*). Its anterior border is separated by a narrow synchondrosis from the basisphenoid (*B.Sph*), while by its antero-lateral borders it is similarly related to the prootics (*Pr Ot.*), and by its postero-lateral borders with the exoccipitals (*Ex Oc*). Its dorsal surface is nearly flat, its ventral surface bears, immediately cephalad of the condyle, a transversely oval depression.

The exoccipital is already partly ankylosed to the periotic. Externally it forms the greater part of the ventro-lateral region of the posterior surface of the cranium (fig. 53), but internally (fig. 56) it appears only as a narrow strip of bone bounding the foramen magnum. It is produced laterad into a large paroccipital process (*pa oc pr*) covered with cartilage, which forms the posterior wall of the tympanic cavity (fig. 77). On its inner or cranial surface (fig. 56) it is separated from the opisthotic by a deep groove, in which is situated—bounded on all sides by the exoccipital—the foramen for the ninth and tenth nerves (*Nv IX, X*). The twelfth nerve makes its exit through a number of small foramina (figs. 51 and 76, *Nv XII.*) in the postero-inferior region of the bone. Part of the horizontal semicircular canal (*HSC*) lies in the exoccipital, and the vertex of the anterior canal (*A.S.C.*) is situated at its junction with the prootic and supraoccipital.

The *supraoccipital* (*S.Oc.*) is a squarish bone articulating by its dorsal border with the parietals (*Pa.*), separated laterally by synchondroses from the exoccipitals and periotic (fig. 56), and ventrally forming the upper border of the occipital foramen. For the greater part of its extent it is extremely thin, but its ventral border is thickened and hollowed out by air cavities continuous with those of the periotic



(figs 75 and 77, *pn c*), and its lateral border bears a deep pit for the vertex of the anterior semicircular canal

The *prootic* (*Pr Ot*) is already fused in great part with the exoccipital, the two bones being inseparable after prolonged maceration, although the bands of cartilage separating them are well shown on the inner surface of the skull (fig 56). It is a large irregular bone, appearing but little on the outer surface, where it forms the mesial wall of the tympanic cavity (fig 52), but internally forming a great part of the postero-ventral region of the brain-case (figs 56 and 75). Its dorsal surface is flattened, and produced mesiad into an obliquely horizontal ridge, which extends from the junction of the prootic, exoccipital, and supraoccipital forwards and downwards to the trigeminal foramen (*Nv V<sup>2,3</sup>*). Under the eaves of this ridge on the mesial surface of the prootic are two recesses, the hindmost of which is the deep floccular fossa (fig 56, *flc f*), while the foremost is a shallow groove containing anteriorly a foramen for the exit of the seventh nerve (*Nv VII*), and posteriorly two small apertures for the eighth (*Nv VIII*). Ventrad and slightly caudad of the auditory foramina are three small apertures, which transmit lesser branches of the eighth nerve. The flattened dorsal surface of the prootic presents low elevations, marking the positions of the anterior and horizontal semicircular canals (*A S C*, *H S C*), these are best seen when the chondrocranium is examined in turpentine by transmitted light. Its posterior face is closely applied to the exoccipital, with which it is partly ankylosed, and between the two bones the dorsal edge of the chondrocranium presents a large trough-like pneumatic cavity (figs 75 and 77, *pn c*), divided transversely by a bridge of cartilage, and closed in the entire skull by the juxtaposition of the parietal and squamosal (figs 62 and 69, *pn c* and Plate 14, fig 170). The lateral surface of the prootic furnishes the inner wall of the tympanic cavity, it is honey-combed with air cells, and presents dorsally a circular facet covered with cartilage (figs 76, 77, and 78, *qu<sup>1</sup>*) for the inner articular process of the head of the quadrate (fig 79, *pr ot*). Near the boundary of the prootic with the exoccipital is the fenestral recess, containing the fenestra ovalis (fig 77, *f<sup>o</sup>ov*) and the fenestra rotunda (*f<sup>o</sup>rot.*), and a short distance cephalad of this recess is the aperture (figs 56, 77, and 78, *Nv VII<sup>1</sup>*), by which the portio dura enters the tympanic cavity.

The *opisthotic* (fig 56, and Plate 14, fig 171, *Op Ot*) is clearly seen on the inner surface of the auditory capsule, as a narrow bone wedged in between the prootic and the exoccipital, and separated from each by a very narrow synchondrosis. In its deeper portion it is ankylosed to these bones.

There is no trace of epiotic or sphenotic ossifications, both of which occur in the Chick (44, pp 242 and 249) at the time of hatching or a little later.

The *basisphenoid* (*B Sph*) which is already completely united with the parasphenoid (basitemporal, *B Tmp*, and rostrum, *Rost*) has an irregularly hexagonal form as seen from above (fig 75), and is wedge-shaped in sagittal section (fig. 56), being quite thin where it joins the basioccipital, and increasing in thickness towards



the pituitary region. By its posterior border it is connected by synchondrosis with the basioccipital, by its postero-lateral border with the prootics, by its antero-lateral borders with the alisphenoids, and by its anterior border with the presphenoid. Immediately caudad of the vertical posterior edge of the presphenoid (fig 56, *Pr.Sph.*) the dorsal surface of the basisphenoid is deeply excavated to form the transversely oval pituitary fossa (*Pty F*)

Ventrally, as already stated, the basisphenoid is completely fused with the elements of the parasphenoid. Of these, the *rostrum* (*Rost.*) is a slender bone crescentic in cross section (Plate 13, figs 155-160) and closely applied to the ventral edge of the mesethmoid. The *basitemporal* (*B Tmp*) projects beyond the basisphenoid both caudad and laterad, forming paired processes which overlap the basioccipital (figs 51 and 76). Between these wing-like processes the posterior edge of the bone is emarginate, and in one specimen presents a small median notch (fig 76, *p ber.fo*) indicating the position of the closed posterior basicranial fontanelle (*cf* Plate 10, figs 108 and 109, and Plate 14, figs 173 and 174, *p ber.fo*). Laterally, the combined basi- and para-sphenoid is produced into the paired outstanding basipterygoid processes (*B ptg pr.*), which are tipped with cartilage, and immediately caudad of these are the pretemporal wings (figs. 51, 76, and 78, *Pr.Tmp.*), which, closely applied to the prootics, help to enclose the anterior tympanic recesses.

On the ventral surface of the basitemporal are paired oblique grooves (figs. 51, *Eus T*) traceable backwards into the tympanic cavities, they lodge the Eustachian tubes, and in later stages become arched over by bone. In the postero-lateral region of the bone is the well-marked carotid foramen (*Int Car.*). This leads into a canal which passes forwards, upwards, and inwards, to open with its fellow into the posterior region of the pituitary fossa immediately beneath the dorsum sellæ (fig. 56, *Int.Car*).

On the dorsal surface of the basisphenoid, near the middle of its antero-lateral border, is the minute foramen for the sixth nerve (fig. 75, *Nv. VI.*), it leads into a canal which passes forwards and slightly upwards and outwards and enters the orbit immediately ventrad of the orbito-nasal foramen (figs 52 and 77, *Nv. VI.*).

Immediately dorsad of the basipterygoid process is a small round foramen (fig 77, *na*) which leads into the interior of the basisphenoid: it probably transmits a nutrient artery

Further particulars of the internal structure of the basisphenoid will be given in the description of the skull in stages H and I (pp 66 and 70). My material did not allow of my making thin sections of the present stage, and, indeed, such a course was unnecessary as the differences between stages H, I, and K are comparatively slight.

The *alisphenoid* (*Al Sph*) is an irregular concavo-convex bone united by cartilage with the anterior border of the prootic and with the antero-lateral border of the basisphenoid. Between it and the prootic is a large rounded foramen (*Nv. V.<sup>2,3</sup>*) for the

exit of the second and third divisions of the trigeminal, on the inner surface of the skull this foramen lies immediately in front of the anterior termination of the prootic ridge, externally it is just above the anterior tympanic recess. From the anterior border of this trigeminal foramen a groove is continued forwards on the inner face of the synchondrosis between the alisphenoid and basisphenoid, and ends in a foramen (*Nv. V.*<sup>1</sup>), which enters the orbit and transmits the first division of the fifth nerve, it may, therefore, be called the orbito-nasal foramen. It is erroneously stated by OWEN (24, p 28) that the first division of the fifth passes out along with the optic, oculomotor, and abducent nerves through the optic foramen, and that the second and third divisions make their exit respectively through the "foramen rotundum" (= orbito-nasal foramen) and "foramen ovale" (= trigeminal foramen). The actual condition of things I have verified both by dissections, and by a complete series of microscopic sections of stage H.

On the outer surface of the cartilaginous junction between the prootic and alisphenoid, and extending on to the latter bone itself, is a rounded, slightly concave cartilaginous facet (fig 78, *qu*<sup>2</sup>), in contact with but clearly distinguishable from a similar facet to be described hereafter (p 54) on the squamosal (*qu*<sup>3</sup>). To this double surface is articulated the external process of the head of the quadrate (fig. 79, *sq*).

The anterior sphenoidal region of the skull is wholly cartilaginous, there being neither pre- nor orbito-sphenoidal ossifications. The *presphenoid* (*Pr Sph*) is represented by a vertical plate of cartilage which passes insensibly into the mesethmoid (*M Eth*, fig 56) in front, and behind is continuous by its lower fourth with the basisphenoid. Its ventral border is thickened and underlaid by the rostrum (fig 159, *Pr Sph*, *Rost*), its dorsal border is produced laterad into small paired wings of cartilage (fig 75, *Pr Sph*), each of which is continued into a narrow band of the same tissue (*Orb.Sph*) passing outwards and slightly backwards to unite with a small bony process on the anterior border of the alisphenoid. The study of earlier stages shows that these outgrowths of the presphenoid are the greatly reduced orbito-sphenoid plates (*cf* Plate 9, fig. 85, Plate 10, figs. 96, 97, 104, 105; and Plate 11, figs 123 and 125, *Orb Sph*).

The optic foramina (*Nv. II*) are situated in the pituitary fossa, one on each side of the presphenoid, their mesial borders being about 3 mm apart. Each is bounded above by the orbitosphenoid bar, below by the basisphenoid, in front by the presphenoid and antorbital plate (*vide infra*), and behind by the alisphenoid. The third and fourth nerves make their exit through the connective tissue filling up the posterodorsal region of the optic foramen, the fourth lying dorsad and slightly laterad of the oculomotor.

The *mesethmoid* (*M Eth*), as already stated, is continuous behind with the presphenoid. In its posterior region it is a plate of considerable vertical extent, and its dorsal border, which is concave from before backwards (fig 56), separates the olfactory

fossæ from one another, and has the relations of a crista galli (figs 75 and 77). At its anterior end the crista galli is produced into a pointed process (figs 56 and 77, *tg pr*), which, as my Father has pointed out, is to be looked upon as a vestige of the cartilaginous tegmen crani of the lower Vertebrata it may be conveniently called the tegmental process. At the apex of this process the mesethmoid reaches the outer surface of the skull (fig 56), and, with the adjacent portions of the ectoethmoids, forms a lozenge-shaped area (fig 50, *Eth Pr Sph*) between the posterior ends of the nasals. Cephalad of the tegmental process the mesethmoid gradually diminishes in vertical extent, becoming, in the anterior portion of the beak, the pod-like prenasal cartilage (*Pr Na*). It is for the most part more or less pyriform in transverse section, its ventral border being greatly thickened (Plate 13, figs 152-158). None of my specimens of this stage, or, indeed, of any other except G (see p. 126), show any trace of the fenestra in the mesethmoid figured by BLANCHARD (6).

No clear distinction can be drawn between aliethmoid, aliseptal, and alinasal cartilages (*cf.* 31) any more than between presphenoid, mesethmoid, septum nasi, and prenasal. The dorsal border of the mesethmoid, from the tegmental process forwards to within about 2 cm of the end of the beak, sends off horizontal plates on each side (figs. 75-77 and Plate 12, figs 152-156, *Ec.Eth.*). These pass at first outwards, then downwards, and finally, in a portion of their extent, inwards, thus forming the roof, the outer wall, and in part the floor of the olfactory chambers. They may be called by the general name of ectoethmoidal plates.

The precise relations of the ectoethmoids vary in different regions, and it is convenient to consider them as consisting of five portions. In the fifth or posterior portion (*Ec.Eth.* 5), besides passing outwards and downwards, they sweep directly backwards, thus forming an almost complete shell-like covering for the principal portion of the olfactory organ, *i.e.*, that part which extends backwards into the orbits (see especially fig 77, *Ec.Eth.* 5). To this region of the ectoethmoidal plate the name aliethmoid might be restricted. Each aliethmoid is a thin plate of cartilage with convex lateral and caudal (posterior) surfaces, its lateral surface is dilated anteriorly, so as to form the well-marked convexity against which, in the entire skull, the lacrymal is applied (figs. 50, 52, 75, 77, *Ec.Eth.* 5, *Lac*); its dorsal border, which is concave from before backwards, forms the outer or lateral boundary of the olfactory fossa (figs 75 and 157), its posterior border is closely applied to the presphenoid and becomes fused with it dorsad, its ventral border is in close contact with the presphenoid and mesethmoid immediately dorsad of the rostrum; its flattened ventral surface (fig. 76) ends in front at its junction with the fourth portion of the ectoethmoid (*Ec.Eth.* 4), and presents a deep emargination which separates a slender forwardly directed process (figs. 76, 77, and 157, *a.*) from the main part of the cartilage. It is the posterior face of this cartilage which forms the anterior wall of the orbit, and is often called the antorbital plate.

In its fourth portion (*Ec.Eth.* 4) the ectoethmoid furnishes only roof and side

walls to the olfactory chamber, not being turned inwards to form a floor for the cavity as a consequence of this, the turbinals are here visible in a ventral view of the entire chondrocranium (figs 76, 155, 156) Immediately cephalad of its junction with the fifth portion, the lateral region of the fourth is sunk inwards so far as to form an obliquely longitudinal depression (figs 76 and 156, *A A Trb*) of considerable depth, and lying, in the entire skull, at about the level of the descending process of the nasal (*cf* figs 56 and 77) The invagination thus produced projects into the olfactory chamber as the anterior accessory turbinal (*vide infra*, p 50), and lodges the antero-dorsal branch of the antrum of HIGHMORE

In its third portion (*Ec Eth 3*) the ectoethmoid is again turned inwards ventrally in the form of a plate with a straight mesial border abutting against the mesethmoid, and with oblique anterior and posterior edges (figs 76, 153 and 154, *Ec Eth 3*) At the anterior end of this plate, near its ventral border, is a small arterial foramen

The second portion of the ectoethmoid (*Ec Eth 2*), like the fourth, furnishes only a roof and outer wall to the olfactory chamber (figs 76 and 152) Lastly, in its first or anterior portion (*Ec Eth 1*) it is unconnected with the mesethmoid (prenasal), and has the form of an obliquely placed band of cartilage which is continued to the end of the beak, passing dorsad of the nostril, curving outwards as it does so, and then turning gently downwards, hookwise, immediately cephalad of the anterior termination of the olfactory sac (figs 75-77 and 149-152) To this plate the name alinasal might be applied, but owing to the unique position of the nostrils in *Apteryx* the relation of this as of other parts of the olfactory capsule is strikingly different from what we are familiar with in other birds

There is a single ethmoidal ossification (figs. 50, 56, 75, 77, *Eth Pr Sph*) in the form of a bone composed of horizontal and vertical portions, and therefore T-shaped in transverse section The horizontal portion (fig 75) is shield-shaped, and appears on the surface of the skull between the posterior ends of the nasals (fig 50) it is marked dorsally by a pair of sigmoid grooves (fig 75) laterad of which it is covered, in the entire skull, by the nasals. The vertical portion ossifies the whole postero-dorsal region of the mesethmoid (fig. 56) and ends below in a rounded border The bone in question is obviously partly mes- and partly ecto-ethmoidal moreover, it subsequently extends caudad so as to ossify the presphenoid, so that it may be conveniently called the *ethmo-presphenoid*

One of the most striking characteristics of the skull of *Apteryx* is the extreme complexity of the turbinals When the mesethmoid is removed (fig 57) there are seen in the olfactory chamber proper four well-marked obliquely vertical folds, while a fifth is continued into the narrow or respiratory portion of the nasal cavity The three hindmost of these folds are perfectly distinct from one another, and I propose to call them respectively the *anterior* (*A Trb*), *middle* (*M.Trb*) and *posterior* (*P.Trb*) turbinals. The fourth and fifth folds are intimately connected with the anterior turbinal I call the uppermost of the two, which forms part of the olfactory region,

has *anterior accessory turbinal* (*A A Trb*), and that which extends forwards, and has no olfactory function, the *ventral accessory turbinal* (*V.A.Trb*.)

In describing these complex structures it will be necessary to refer, not only to dissections, but to transverse and horizontal sections (Plates 7 and 11).

The posterior turbinal (figs 57, 75, 83, 84, and 158, *P.Trb.*) has the form of a scroll attached by the whole of one edge to the aliethmoid. It is rolled upon itself caudad (fig 83) forming about one turn. Like the other turbinals its line of attachment is oblique, passing from above forwards, as well as downwards.

The middle turbinal (figs 57, 75, 83, 84, 157, and 158 *M Trb.*), is also attached along the whole length of one nearly vertical edge. from its attachment it passes at first mesiad (fig 83), then turns caudad, then laterad, then mesiad again, and passes cephalad as a broad plate somewhat indented in the middle by a vertical furrow, which gives it the appearance when viewed from its inner face (fig 57) of a double fold. The broad vertical plate thus formed is attached to the aliethmoid along the anterior part of its ventral border, but is free dorsad, its apparent connection with the dorsal wall of the olfactory chamber in fig 57 being due to the fact that the mucous membrane is not removed. anteriorly it is rolled upon itself caudad (figs. 83 and 84), forming a scroll of one turn, which is attached to the aliethmoid above and below, but is free in the middle.

The anterior turbinal (figs 57, 75, 83, 84, and 157, *A.Trb.*) arises as a single, somewhat oblique plate from the aliethmoid. Soon after its origin it turns caudad (fig 83), then cephalad, then caudad again, and finally curves forwards, forming a single oblique scroll with an in-turned anterior border.

The anterior accessory turbinal (figs 57, 77, 83, 84, 155, and 156, *A.A.Trb.*), arises dorsally as a narrow plate springing from the anterior turbinal near its origin (fig 83), it passes forwards and downwards, and merges into the hollow ingrowth of the ectoethmoid mentioned above (p. 49, figs. 84, 155, and 156). It thus happens that the main part of the anterior accessory turbinal is not a plate-like ingrowth, but an actual hollow invagination of the ectoethmoidal wall. In it, as already mentioned, is inclosed the antero-dorsal branch of the antrum of HIGHMORE. At its anterior and ventral end this pouch gradually narrows, and passes insensibly into a plate of cartilage, which joins the ventral accessory turbinal, gradually fading away on the dorsal surface of the latter.

The ventral accessory turbinal (figs. 57, 76, and 153-156, *V.A Trb*) consists of a horizontal plate of cartilage attached along its whole length to the ectoethmoid, and connected caudad with the ventral border of the anterior turbinal. At its posterior end it is a simple narrow plate, but soon divides into two plates, a dorso-mesial and a ventro-lateral (fig. 155), which continue forwards, enclosing between them a dihedral angle. The dorso-mesial plate is rolled upon itself dorsad, and comes to an end a short distance in front of the anterior end of the anterior accessory turbinal (fig. 57). The ventro-lateral plate is rolled upon itself ventrad, and is continued forwards,



undergoing a gradual simplification of structure, as far as the junction of the second and third portions of the ectoethmoid (fig 153)

As already mentioned, all the turbinals, with the exception of the ventral accessory, are covered with Schneiderian membrane, and are therefore analogous to the ethmo-turbinals of a mammal. The ventral accessory turbinal is covered with ordinary mucous membrane, and belongs to the merely respiratory portion of the nasal chamber—it may be compared with maxillo-turbinals of mammals

There is also, separated by a considerable interval from the turbinals proper, a fold which may be compared with the naso-turbinal of mammals. This (fig 151, *Na.Tr.b*) is a narrow, horizontal, shelf-like plate of cartilage springing from the inner face of the first or anterior portion of the ectoethmoid, and extending from a little in front of its junction with the second portion as far forwards as the nostril

It may be mentioned in this connection that the lining of the nasal sac from the nostril nearly as far back as the junction of the second and third portion of the ectoethmoid—i.e., the preturbinal portion of the olfactory chamber—has the character rather of skin than of mucous membrane, its epithelial layer consisting of a stratum Malpighi covered by a very thick stratum corneum closely resembling, and actually exceeding in thickness, the horny beak (see Plate 12, fig 151)

On each side of the ventral edge of the mesethmoid in the vomerine region, i.e., from about the posterior end of the third to the middle of the fifth portion of the ectoethmoid, is a slender rod of cartilage (figs. 76, 77, and 155–157, *Ja C*), imbedded in connective tissue, and lying parallel to and either immediately dorsad or slightly laterad of the dorsal edge of the trough-like vomer. It is about 10 mm long, and about 0.14 mm in diameter, and is most easily made out in sections, although when once its position is known, it can be readily prepared in a well-macerated skull by carefully removing the vomer. It is obviously the vestigial cartilage of JACOBSON'S organ, first described by my Father in *Rhea* (30), and afterwards in various Passerine Birds (36).

The *quadrate* (tympanic, OWEN\*) has practically the same form as in the adult. The otic process (fig. 79, *ot pr.*) bears a large transversely elongated articular head covered with cartilage, and having its mesial extremity widened antero-posteriorly. This portion of the head of the quadrate bears a well-defined, nearly circular, slightly convex facet (*pr.ot*) for articulation with the surface already noticed on the prootic (p 73, fig. 78, *qu.*<sup>1</sup>). The lateral narrow portion of the head of the quadrate (fig 79, *sq*) articulates in front with the surface already noticed on the alisphenoid (p 78, fig 78, *qu.*<sup>2</sup>), and behind with a small cartilage-covered facet on the squamosal (p 97, fig. 78,

\* The revival by GADOW (12) of the Okenian hypothesis of the homology of the sauropsidan quadrate with the mammalian tympanic is an instructive instance of the way "the whirligig of time brings in his revenges". One had lately been content to think that this question was finally settled in 1869 in favour of the REICHERT-HUXLEY view, or some modification of it

*qu*<sup>3</sup>) Thus, in *Apteryx*, the quadrate can by no means be described as having a single-headed otic process

The orbital process (*orb pr*) is tipped with cartilage. The shaft of the quadrate bears on its posterior surface a large pneumatic foramen (*pn f*) leading obliquely downwards and forwards into a cavity excavated in the interior of the bone. Ventrally the quadrate is tipped with cartilage, and bears the usual two condyles, one (*cn 1*) mesiad and slightly cephalad of the other (*cf*, fig 51). Lying almost immediately cephalad of the external condyle is a deep hemispherical cavity for the articulation of the quadrato-jugal, while dorsad of the internal condyle, and at the base of the orbital process is a somewhat ill-defined surface for articulation with the pterygoid.

The *articular* (figs 54-56 and 80, *Art.*) is a concavo-convex bone, largely covered with cartilage both doisad and laterad. From its anterior border the long slender MECKEL'S cartilage (*Mck. C.*) is continued forwards and slightly inwards until it reaches the posterior end of the long mandibular symphysis, when it turns directly forwards, and passes parallel to and in close contact with its fellow of the opposite side to within a short distance of the end of the beak (*cf* figs. 151-160). There is no trace of a basi-mandibular element.

The *stapes*, or columella auris (fig 81), is not described by OWEN. It consists of the usual oval plate of bone (*Col*) inserted in the fenestra ovalis, and continued into a short bony rod, which passes outwards and forwards, and bears at its distal end a triradiate cartilage, the extra-columella (*Ex Col*) of GADOW (11). The middle of the three rays, or extra-stapedial (*E St*) continues the direction of the bony columella, and is fastened distad to the inner surface of the tympanic membrane. The second ray, or supra-stapedial (*S St*), is dorsal and posterior in position, and has its extremity thickened and produced into a small retral spur directed ventrad; it is also attached to the tympanic membrane. The third ray, or infra-stapedial (*I. St*), springs from the ventral region of the extra-columella close to its proximal end, and immediately opposite the supra-stapedial. it passes forwards and downwards to the anterior tympanic recess, where it becomes ligamentous. In serial sections of Stage H it can be traced to a point about 0.75 mm dorsad of the internal angle of the articular, beyond which it disappears as a distinct structure.

The *tongue-bone*, or so-called hyoid (fig. 82), consists of a median sagittate cartilage (*B Br*) called basi-uro-hyal by my Father (28), produced backwards into a slender-pointed rod. With the lateral processes of this cartilage are articulated the posterior cornua, each of which consists of an ossified ceratobranchial (*C.Br.*) with cartilaginous ends, and of an unossified epibranchial (*E.Br.*) pointed distad. Imbedded in the extremity of the tongue is a Y-shaped cartilage, having its stem (*B Hy*) directed forwards, while its arms (*C Hy*.) extend backwards and embrace the median cartilage (*B.Br.*). the point of the latter is connected by ligament with the re-entering angle of the Y. This answers to the heart- or arrow-shaped cartilage

found in most birds, and considered by my Father as being formed of partially coneresced ceratohyals

I am disposed to take a different view of the composition of the avian "hyoid" I consider the arms of the Y-shaped cartilage (*CHy*) to be ceratohyals, and its median portion or stem (*BHy*), the basihyal, formed as it obviously is by concrescence of the right and left halves of the hyoid arch. The sagittate cartilage (*BBr*) I consider to be the first basibranchial

According to this view there is no concrescence between the hyoid and first branchial arches in *Apteryx*, they remain united only by ligament, so that in preparing the skeleton by maceration the first branchial (so-called hyoid) readily separates, leaving the true hyoid imbedded in the end of the tongue, where it is easily overlooked. Moreover, the hyoid is obviously obsolescent; as will be shown, it chondrifies late and never ossifies

### *The Membrane Bones*

The *parietal* (fig 62) is an irregularly four-sided concavo-convex bone. By its straight mesial border it is joined by membrane to its fellow of the opposite side (fig 50) its sigmoid anterior border articulates with the frontal, and its irregular lateral border with the squamosal, while its irregular posterior border abuts against the occipital cartilage partly in the supra- and partly in the ex-occipital region (fig 53). At its postero-lateral angle is a pit (*pn c*) which fits over and closes above the hinder division of the pneumatic cavity in the prootic (figs 75 and 77, *pn c*)

The *frontal* (fig 63) is a very irregular concavo-convex bone, broadest at its posterior end and narrowing cephalad. By its evenly curved posterior border it articulates with the parietal, its nearly straight mesial border is separated from that of its fellow of the opposite side by membrane (fig 50), its arched lateral border, straight as seen from below, articulates with the alisphenoid. In front it is produced into a narrow nasal process (*na pr*), which articulates with the postero-lateral border of the nasal. Immediately cephalad of its alisphenoid border the frontal is produced into an orbital process (*orb pr*), which curves downwards and inwards and abuts against the alieethmoid (fig 52), from its antero-ventral angle is sent off an irregular orbitosphenoid process (*o.sph pr*), which passes directly mesiad and overlies the orbitosphenoid bar (fig. 56, *o sph pr*). Thus the frontals nearly meet in the middle line over the presphenoid, reminding one of the arrangement found in some of the Primates

Immediately cephalad of the orbital process is a large notch, covered in the entire skull by membrane, and converted into a foramen, the superior orbital fontanelle (fig 52, *S.orb.F*), by the juxtaposition of the alieethmoid. From the dorsal border of this foramen a pedate descending process (*d pr*) is given off, and passing downwards and slightly forwards, abuts against the convex lateral surface of the



aliethmoid The orbitonasal nerve passes immediately mesiad of this process in its course from the orbit to the nasal cavity

The *squamosal* (fig 69) is a roughly triangular bone articulating by its sinuous dorsal border with the parietal, by its concave anterior border with the alisphenoid and by its thickened ventral border with the prootic and exoccipital. Its ventral region is hollowed out into a pneumatic cavity (*pn c*), which in the entire skull fits over the anterior division of the hollow in the prootic already described (p 45, figs 75 and 77, *pn c.*, and fig 170), the posterior division, as already stated, being covered by the parietal. The antero-ventral angle of the squamosal is produced into a triangular zygomatic process (*zyg pr.*) which is directed forwards and downwards immediately laterad of the otic process of the quadrate (fig 52). Just mesiad of the base of this process the squamosal bears on its antero-ventral angle an articular facet covered with cartilage (*qu<sup>3</sup>*) for the posterior surface of the external division of the head of the quadrate. Caudad of this facet, the ventral edge of the squamosal is perforated by a considerable aperture (indicated by a bristle in fig 69) by which the air-cells just mentioned communicate with the tympanic cavity (*cf.* fig 78, *qu<sup>3</sup>*, *pn c.*, and figs 169 and 170).

With regard to the cartilaginous facet *qu<sup>3</sup>* it is an interesting question whether the presence of a distinct chondrite developed in connection with a parostosis is an indication that the latter is phylogenetically a cartilage bone, like the palatine and pterygoid of *Sauropsida* and *Mammalia*, or whether the chondrite in such cases is to be considered as a neomorph. In any case the cartilage now under consideration is comparable and may possibly be homologous with the meniscus of mammals, while it certainly corresponds with the cartilaginous facet on the squamosal of lizards (33).

The *nasal* (fig 66) is a long narrow bone crescentic in cross section (Plate 13, fig. 155), pointed in front, and irregularly truncated behind. By its posterior border it articulates with the frontal, and by the greater part of its mesial border with the nasal process of the premaxilla. caudad of that process the nasals diverge so as to allow the central part of the ethmo-presphenoid to appear (fig. 50). From the posterior end of the lateral border of the nasal springs a slender descending process (*d pr*) which takes a direction downwards and slightly forwards, abutting against the ectoethmoid and articulating caudad with the lacrymal (figs 50 and 52).

The *lacrymal* (fig 68) is a small irregular bone consisting of a shell-like central portion applied to the surface of the aliethmoid (fig. 52), and of an ascending portion which articulates with the descending process of the nasal. It is perforated obliquely by the lacrymal foramen (*lac for*).

The *premaxillæ* (fig. 59) are already ankylosed together, forming a long triradiate bone. The common portion or body of the bone is small and rounded, forms the tip of the beak, and is honey-combed with small close-set pits in which are end-organs abundantly supplied by branches of the dorsal ramus of the orbitonasal nerve. The nasal process (*na pr*) is also single, except at its posterior end, where there is a longitudinal cleft. The palatine processes (*pal.pr.*) are quite distinct, each being

attached to the body of the bone by a narrow neck, widening as it passes backwards, and finally dividing into a short mesial, and a long lateral process, both of which articulate with the maxilla. The external nostril lies at the junction of the nasal and palatine processes with the body.

The *maxilla* (fig 58) is a long flat bone pointed in front where it is underlaid by the palatine process of the premaxilla. It gradually widens as it passes backwards and divides into two processes, an internal or palatine (*pal pr*), and an external or jugal process (*ju pr*). Mesial of the anterior end of the palatine process is a groove bounded dorsad by an extension of the inner margin of the bone, and serving for the reception of the palatine (*cf* figs 50 and 51). The outer border of the maxilla forms part of the boundary of the upper jaw, by its inner or mesial border it articulates with its fellow for a short distance in front, afterwards separating from it so as to leave a narrow lanceolate interval partly filled up by the vomer. The palatine process of the maxilla underlaps the palatine bone towards its outer border; the jugal process articulates dorso-laterad with the jugal.

The *jugal* (fig 70) is a slender rod-like bone, articulating by its anterior half with the jugal process of the maxilla, and behind articulating by its dorsal surface with the quadrato-jugal.

The *quadrato-jugal* (fig 71) is a slender bone, pointed in front where it underlies the jugal, and thickened posteriorly where it articulates with the pit already noticed on the quadrate (p 52) by a knobbed extremity (*qu*) covered with cartilage (see also fig 165, *Qu Ju*). This is a second instance in the skull of *Apteryx* of a parosteal bone provided with a cartilaginous articular end.

The *vomer* (fig. 60) is Y-shaped, consisting of a median anterior limb and slightly diverging posterior limbs. The anterior limb which projects between the maxillæ is trough-like, and pointed in front, the posterior limbs have their ventral surfaces slightly concave from side to side, and their posterior ends forked. Each articulates at its hinder end dorsad with the pterygoid and ventrad with the palatine (see also figs 155-157).

The *palatine* (fig 61) is of very irregular form, its pointed and jagged anterior end fits into the groove on the inner border of the maxilla, the palatine process of which is applied to the whole length of its ventro-lateral surface. Its posterior end is expanded and obliquely truncated. It underlies the hinder end of the vomer, and articulates laterad with the pterygoid.

The *pterygoid* (fig 67) terminates caudad in a saddle-shaped surface covered with cartilage (*qu*) for articulation with the quadrate. The posterior end of the bone has the form of a stoutish rod, somewhat flattened from above downwards, and bears on its mesial surface a slightly elevated, longitudinally oval facet (*b ptg pr*), covered with cartilage, for articulation with the basipterygoid process. The anterior two-thirds of the bone is flattened from above downwards, and produced dorsad into an obliquely longitudinal ridge, and divided anteriorly into mesial and lateral processes.

The mesial process articulates with the lateral border of the vomer, and with the posterior expanded portion of the palatine, the lateral process articulates with the dorso-lateral border of the palatine, and of the palatine process of the maxilla

The *dentary* (fig 72) is already ankylosed with its fellow of the opposite side, forming a symphysis about 1.5 cm long. The symphyseal portion of the united bones is narrow, deeply grooved longitudinally on its dorsal surface, and pitted below (fig 55) like the corresponding part of the premaxilla. Each ramus consists of a horizontal dorsal plate, and an oblique ventral plate, the two joining laterad in an acute dihedral angle. Posteriorly these two plates are separate, and form slightly divergent dorsal and ventral processes.

The *splenials* (fig 64) are also ankylosed, forming a symphysis nearly 1 cm long. Each has a nearly flat mesial and a strongly-grooved lateral surface. Thus, when the dentary and splenial are placed in position, they enclose between them a longitudinal canal for MECKEL'S cartilage (fig 153).

The *angular* (fig 65) is a narrow splint-like bone, with its broad, flattened posterior end applied to the mesio-ventral region of the articular (figs 55 and 56). The main part of the bone extends forwards between the splenial and the ventral process of the dentary, forming the posterior portion of the ventral edge of the mandibular ramus.

The *supra-angular* (fig. 73) has its broad, irregular, somewhat thickened posterior end applied to the ventro-lateral region of the articular (figs 52 and 55). The rest of the bone is a narrow slightly-twisted splint, which extends forwards between the splenial and the dorsal process of the dentary.

The *coronary* (fig 74) is a slender, rod-like bone, somewhat broadened and truncated at its posterior end and pointed in front. It lies on the inner face of the mandibular ramus (figs 54 and 56) near its articular end, between and nearly parallel with the angular and supra-angular.

The relations of both cartilage and membrane bones are well shown in the series of sections of Stage H (Plates 12-14).

### *b Development of the Skull.*

#### *Stage A* (Plate 4, figs 17-21)

The parachordal region or investing mass is represented by a plate of dense blastema on each side of the notochord, and extending a short distance cephalad of its anterior end as the "middle trabecula" of RATHKE (fig. 17, *Pr.Ch*). This name my Father (29) proposes to drop, as the structure in question has nothing to do with the trabeculae cranii. As, however, a distinct chondrite subsequently appears in it, which gives rise to part of the dorsum sellae, and as it is apparently the first part of the skull to appear, being at the present stage decidedly better marked than the parachordals, I think it will be convenient for descriptive purposes to speak of it as the *prochordal plate*.

The end of the notochord (*Nch*) is simply upturned, not bent into a hook-like form as in Selachians (2, 47), or twisted as in *Chelone* (35). The next stage shows this very clearly, since the notochord never appears twice in the same transverse section (figs 24 and 25).

There is a concentration of the mesoblastic tissue in the visceral folds (figs 19–21), but the visceral arches can hardly be said to be formed as yet.

#### *Stage B* (Plate 4, figs 23–30)

The prochordal plate has become a very distinct unpaired structure (fig 23, *Pr Ch*), reaching from the end of the notochord, dorsad between the metencephal (*Mt cæ*) and diencephal (*Di cæ*). The third nerve (*Nv III*) passes through it in its course from the base of the mid-brain. A very short distance caudad of the junction of the prochordal with the parachordal plates the latter are seen to be distinctly paired (figs 25 and 26, *Pu Ch*), the thickenings of mesoblast which form them not meeting either above or below the notochord. Except at their extreme anterior limit (fig 24) the parachordals remain thus distinct through their whole extent (figs 25–30), and are uniformly less well-marked than the prochordal.

In the auditory region the thickened mesoblast of the parachordals is seen to be extending laterad, so as to invest the auditory sacs (fig. 28).

The visceral arches (fig 26, *Mn.*, fig 27, *Hy.*) are visible as plates of dense blastema, but, with a single specimen, their precise relations could not be very satisfactorily made out.

#### *Stage C* (Plate 5)

The prochordal plate is still better defined than in the previous stages, and is produced at its free end into paired processes (fig 35, *Pr Ch*), which lie immediately laterad of the oculomotor nerve (*Nv III*). A short distance in front of (above) the end of the notochord, the prochordal forms a well-marked transverse plate (fig 36, *Pr Ch.*), narrow towards the middle line, broadened at either end, and perforated by the third nerve.

I have seen no references to the bifurcation of the “middle trabecula” just referred to. The two processes have exactly the same relation to the main unpaired portion of the prochordal plate as the trabeculæ to the anterior unpaired portion of the parachordals (*vide infra*), and bearing in mind GOTTE’s theory that the trabeculæ represent a pair of neuroids (neural arches), and ALBRECHT’s notion (1) that the dorsum sellæ is a “Wirbelcentrum-complex,” it is tempting to compare these processes also with neuroids. But it yet remains to be seen whether they exist in the lower Vertebrata, and, if so, whether they are independent elements like the trabeculæ, or, as in the present case, mere processes of the prochordal plate.

The parachordals are well defined anteriorly, and have united dorsad of the notochord (fig. 37), but for the greater part of their extent they are still separate (figs

38-42), and have not yet passed into the condition of prochondral tissue. The lateral extensions from the parachordals forming the auditory capsules are well seen in this stage (figs. 39 and 40, *Au c*).

The trabeculæ (fig. 37, *Tr*) have apparently just made their appearance. In sections which include the anterior end of the notochord and the pituitary evagination (*Pty*) of the pharynx, they have the form of short paired rods, springing from the united parachordals, and passing immediately laterad of the internal carotids (*Int car*), so as partly to embrace the pituitary body.

The visceral arches are more clearly marked than in the preceding stage, the mandibular (fig. 38, *Mn*), hyoid (fig. 39, *Hy.*), and first branchial (fig. 41, *Br 1*) being very obvious.

#### *Stage D* (Plate 9, figs. 85-95)

Owing to the unfortunately damaged condition of the single embryo belonging to this stage, my observations are far from complete. The drawings of sections (figs. 88-95) are accurate, only obvious distortions having been corrected, but the figures of the entire skull (figs. 85 and 86) must be looked upon as restorations from very imperfect data.

The cerebral flexure is still nearly a right angle; the sections cut at right angles to the long axis of the beak, become horizontal in the parachordal region (*cf.* figs. 88-93 with figs. 94 and 95). The advance beyond the preceding stage is very marked; all the parts of the chondiocranium are formed, and consist, for the most part, of hyaline cartilage.

The parachordals (figs. 86, 94, and 95, *Pa.Ch*) have to a considerable extent coneresced below the notochord, anteriorly, however, they are still separate, a median slit-like space, the posterior basicranial fontanelle (figs. 86 and 94, *p bcr fo*), being left between them. The anterior boundary of this aperture is formed by the intumed hook-like anterior ends of the parachordals (*y*) which meet in the middle line, and, at the same time, form the posterior limit of the carotid foramina (*Int.car*).

The precise form of the auditory capsules could not be deduced with accuracy from the sections, but it is almost certainly not very different from what we find in the next two stages in which it was made out by dissection.

In the basisphenoidal region (figs. 86, 93, and 94, *B Sph*) the skull-floor is widely open below, the trabeculæ not having united in the middle ventral line. The space thus formed is filled with connective tissue which supports the pituitary body (*Pty*), and through which the internal carotid arteries (*Int.car.*) enter. Cephalad of the pituitary body the trabeculæ are in close contact, save for a thin stratum of prochondral tissue (fig. 92, *B.Sph.*), and each sends off outwards and downwards a large basipterygoid process (*B ptg pr*), the size of which, so much greater proportionally than in later stages, is worthy of notice.

In the posterior presphenoidal region (fig. 91, *Pr.Sph*) the trabeculæ are still

separated by a layer of prochondral tissue, and each sends off dorsad a vertical plate (*Pr Sph*'), which bounds the optic foramen (*Nv II*) in front, and at its dorsal edge is continued into the orbitosphenoid (*Orb Sph*). In later stages, these vertical offshoots of the trabeculæ have united in the median plane to form the impaired presphenoid cartilage (*cf* figs 86 and 91 with figs 98 and 116); their distinctness in the present stage is interesting as showing that the prenasal cartilage or intertrabecula does not extend so far back in Birds as in Crocodiles (34, Plate 63, fig. 4), and Turtles 35, Plate 2, fig. 6).

In the anterior presphenoidal region (fig. 90, *Pr Sph*) the trabeculæ are continued into a single cartilage, pyriform in transverse section, its ventral region is unpaired, and may possibly, though not probably, be formed from a prenasal cartilage, but its dorsal region is still unchondrified in the median plane, and the whole structure appears to be a continuation of the trabeculæ.

The mesethmoid (figs 85, 86, 88, 89, *M Eth.*) is well chondrified below, but the formation of cartilage has not yet extended to its dorsal border, it shows no indication of being formed from paired trabeculæ.

The lateral offshoots of the trabecular region of the skull are already well developed. The ectoethmoids (*Ec Eth.*) are only chondrified posteriorly, they already extend backwards caudad of the middle of the eye (fig. 90). The orbitosphenoid plates (*Orb Sph*) are immense; they spring from the whole length of the long presphenoid region and extend backwards, bounding the optic foramen (*Nv II*) above, as far as the parachordal region. The alisphenoids (*Al Sph*), on the other hand, are comparatively small, and owing to the cerebral flexure their long (anterior-posterior) axis is nearly vertical instead of horizontal. The trigeminal (*Nv V<sup>2,3</sup>*) and orbito-nasal (*Nv V.<sup>1</sup>*) foramina have their usual position between the alisphenoid and the auditory capsule. In these and other points the resemblance of the Kiwi's skull at this stage to that of an embryo Mammal (32, Plate 33, fig. 3), or Crocodile (34, Plate 63, fig. 6), is very striking.

The only indication of the turbinals is an in-pushing of the ectoethmoids immediately over the posterior nares (fig. 89, *AA Trb*). This is the rudiment of the anterior accessory turbinal, which is thus the first of these ectoethmoidal folds to appear.

The quadrate (*Qu*), as far as could be made out from the sections, has a single head articulating with the prootic region of the auditory capsule. The mandible (*Mek C.*) consists entirely of MECKEL'S cartilage, which is expanded at its proximal or articular end.

The columella (figs 87 and 93, *Col*) has its knotted mesial end inserted into the fenestra ovalis, and its outer end or extra-stapedial (*E St*) fixed to the tympanic membrane, near the middle of its length it gives off a slightly curved downwardly directed process, the infra-stapedial. I can detect no trace of supra-stapedial.

The tongue-cartilage (so-called hyoid) consists of a median basibranchial (fig. 90,



*B.Br*) giving attachment laterad to a pair of cerato-branchials. There is no trace of the Y-shaped cartilage of the adult and advanced embryo (fig 82, *B Hy*), which I take to represent the hyoid arch. The late appearance of this structure is a good indication that the hyoid proper of Birds is tending to disappear. It is worthy of notice that cerato-hyals are figured in my Father's second stage of the Chick's skull (31, Plate 81, fig 5), which corresponds roughly in point of development with the KIWI embryo now under discussion, this would seem to show that *Apteryx* is a step nearer atrophy of the hyoid than *Gallus*.

There is no trace of the palato-pterygoid bar described in early embryos of the Chick (31, Plate 81, figs 1, 3, and 5) in *Apteryx* the palatine and pterygoid are in no way distinguishable in their development from the remaining membrane bones.

#### *Stage E* (Plate 10, figs 96-103)

In the single embryo belonging to this stage the brain was removed and the chondrocranium drawn from above and roughly sketched from the side before being sectioned. Hence fig 97 is a drawing of an actual dissection, and figs. 96 and 98, although in part restorations, are correct in all their main features.

The cerebral flexure is now about 120°. The general proportions of the skull are much the same as in the previous stage.

In the parachordal region the notochord (*Nch*) is clearly seen, and is shown by sections to be surrounded with cartilage only in the neighbourhood of the occipital condyle. Elsewhere the parachordal cartilages have not met above the notochord, and their union below it does not extend very far forwards. The occipital arch is completed dorsad by prochondral tissue.

The auditory capsules (*Au C*) have rounded dorsal and mesial contours, laterad they are produced into well-marked paroccipital processes (fig. 96, *pa oc.pr*) bounding the tympanic recesses. The foramina for the facial and auditory (*Nv VII, VIII.*), and for the glossopharyngeal and vagus (*Nv. IX., X*) nerves are well seen, but there is no indication of the floccular fossa.

The pituitary fossa (fig 97, *Pty F.*) is a deep pit with a nearly circular outline, bounded in front by the presphenoidal region and behind by the high dorsum sellæ or postclinoid wall (*Dors sell*), which extends transversely between the alisphenoids. In a dissection such as that from which fig 97 is taken, the fossa appears to be completely bounded by cartilage, but sections show that this is not the case. The middle portion of the dorsum sellæ is formed of connective tissue (fig. 101) in which the upturned end of the notochord is embedded, and the floor of the fossa contains three median fontanelles filled with fibrous tissue continuous with the perichondrium. The hindmost of these (figs 98 and 101, *p.bcr fo.*) is the posterior basiscranial fontanelle already noticed (p 58). It is bounded behind by the notochord (*Nch.*) and its ventral cartilaginous investment, and in front by a transverse bar of cartilage (*y*) which separates it from the next or middle basiscranial fontanelle (*m bcr.fo.*). This

latter looks, in the present stage, almost directly forwards, and is separated from the third or anterior basicranial fontanelle (*abcrfo.*) by another transverse bar of cartilage (*x*). The anterior fontanelle is bounded in front by the presphenoid (*Pr. Sph*), and extending into it from the mouth is seen the remains of the pituitary evagination (fig 101, *Pty ped*). In a section taken very slightly laterad of the median plane (fig 102), the pituitary fossa is seen to be completely bounded by cartilage, both its floor and posterior wall being fully chondrified; the basicranial fontanelles are, therefore, extremely narrow from side to side.

In the Chick my Father figures only two basicranial fontanelles, corresponding with those I have called anterior and posterior (31, Plate 83, fig 2) of the middle aperture I have seen no account in the works of previous observers. My observations are not sufficiently complete to allow of a full explanation of these spaces and of the bars of cartilage which separate them, but after a careful comparison of this with the previous stage, I am disposed to think that fig 103 offers a reasonable theory of this most difficult part of the skull. The figure is diagrammatic, and represents the basi-sphenoidal region on one plane, the cerebral flexure being supposed to be straightened out. The dotted lines show the outlines of the trabeculæ (*Tr.*) and parachordals (*Pa ch*), and it will be seen that I suppose the commissure *x* to be formed by the inturned posterior ends of the trabeculæ, the commissure *y* by the inturned anterior ends of the parachordals described in the previous stage (p 58, fig 94, *y*). In the diagram the upturned end of the notochord (*Nch*) is supposed to be cut off.

The orbitosphenoids (*Orb Sph*) are still very large, although smaller than the alisphenoids (*Al Sph*). The whole preorbitosphenoidal region is saddle-shaped (fig 97), being convex from before backwards, and concave from side to side, with, however, a slight rise in the middle (*cf* fig 116). The anterior border of the alisphenoid overlaps the posterior border of the orbitosphenoid. The presphenoid (*Pr. Sph*) is large, and the paired upgrowths of the trabeculæ which form it have apparently completely concresced, but as this part of the skull was sectioned longitudinally, it is impossible to be as certain on this point as if transverse sections also had been examined.

The posterior part of the ectoethmoidal plate (*Ec Eth.*) is well chondrified, and the three principal turbinals have appeared. The olfactory chamber is continued from the turbinal region to the end of the beak (fig 100) as a narrow tube lined with a low columnar epithelium, and completely filled with cells evidently derived from the proliferation of the epithelium, so that at this stage there is no actual communication between the olfactory sac and the exterior except by way of the posterior nares and the mouth. This is well shown in fig 114, taken from a transverse section of the following stage.

The quadrate (*Qu*) was definitely ascertained to articulate with the auditory capsule by a single head. The columella (fig 99) shows the three processes of the extra-columellar region, owing to the cerebral flexure, the direction of the supra-stapedial



is backwards and downwards. There is still no trace of the hyoid portion of the entoglossal, but both basibranchial and posterior cornua are well chondrified

The position of the future membrane bones is indicated in the sections by deeply-stained patches, formed of close-set mesoblast cells. The rudiments of the palatine and pterygoid are in no way distinguishable from those of the remaining parostoses

*Stage F* (Plate 10, figs 104–119)

The skull of this embryo was partially cleaned by dissection, and sketched from above, from below, and from the left side before being stained and sectioned

The cerebral flexure is greatly reduced, the cranio-facial angle being nearly  $150^{\circ}$ . This, and the elongation of the prenasal cartilage (*Pr Na*) have greatly altered the form of the chondiocranium, which now approaches that of the adult, although still presenting very important differences

The parachordal region has undergone little alteration. There is a large posterior basicranial fontanelle (*p.bcr fo*) filled with connective tissue, which is continued dorsad as the median portion of the dorsum sellæ (*Dors Sell*), and has imbedded in it the anterior end of the notochord (*Nch*). Immediately above the latter, but quite independent of it, is a nodule of cartilage (figs 108, 109, 111, and 112, *Pr.Ch*), evidently formed as a distinct chondrite in the prochordal plate (Plate 2 and 3, figs 17 and 36, *Pr.Ch*). I propose to call it the *prochordal cartilage*. It appears to answer either to the little cap of cartilage which sheaths the end of the notochord in *Chelone* (35, Plate 7, fig 7a), or to the vertical plate, lying altogether dorsad of the notochord (marked *p cl*), and forming the dorsum sellæ. In the present instance it is certainly an independent element of the chondrocranium.

On ALBRECHT's theory (1) that the dorsum sellæ is an "epipituitare Wirbelcentrum-complex," the prochordal cartilage may very fairly do duty for a centrum, the paired processes of the prochordal plate in stage C, representing the corresponding neuroids which atrophy without chondrification, but in the absence of any account of the grounds upon which ALBRECHT's views rest, beyond the short paper referred to, I am not disposed to consider them as very well founded.

The structure of the pituitary fossa is unaltered, the anterior (*a.bcr fo*) and middle (*m.bcr fo*) basicranial fontanelles being very obvious. All three fontanelles are of less width from side to side than the prochordal cartilage, as shown by fig. 112, taken about 0.2 mm from the median plane. The posterior of the two cartilaginous commissures (*y*) separating the fontanelles is now largely caudad of the anterior one (*x*), instead of being altogether below it as in the previous stage (*cf.* figs. 101 and 111); this is an obvious result of the straightening of the skull floor.

The alisphenoids (*Al.Sph*) are somewhat larger than in the preceding stage, the orbitosphenoids are almost unaltered in relative size. The ectoethmoids (*Ec.Eth*) are still largely composed of prochondral tissue (figs 113–115), only their posterior portions (fig 116, *Ec.Eth*. 5) consisting of hyaline cartilage. In addition to the

tubinals present in the previous stage, the ventral accessory fold (fig 115, *V A Trb*) has appeared. Transverse sections of the beak show very clearly the complete filling up of the anterior portion of the nasal chamber with epithelial cells (fig 114).

The quadrate (*Qu*) has undergone no alteration. Its head is still single, articulating only with the auditory capsule, although, as shown by sections, embraced externally by the rudiment of the squamosal (fig 119, *Qu*, *Sq*). In the columella the infra-stapedial is apparently somewhat longer than in the previous stage. The tongue-cartilage still shows no trace of its hyoid portion (fig 110).

The membranous foundations of the membrane bones are now well shown, but no actual ossification has yet appeared. In sections (figs 113–119) the bone-rudiments have very much the appearance of the bones themselves in a later stage after decalcification, except that the matrix, in which the lime salts subsequently appear, takes on a lighter tint with borax-carmin. The identity in mode of development between the palatine and pterygoid and the remaining membrane bones is illustrated by fig 117, in which the rudiments of the quadrato-jugal (*Qu Ju'*) and pterygoid (*Ptg'*) are seen to be of precisely similar character. There is so far no trace of the cartilaginous articular surfaces on the pterygoid, quadrato-jugal, and squamosal.

#### *Stage G* (Plates 11 and 12, figs 120–145)

This is one of the most important stages in the development of the skull, the chondrocranium having practically attained its final form, and nearly all the membrane bones having appeared. I greatly regret that one of the two specimens belonging to this stage (*A owenii*) was so much damaged as to be unreliable except for general purposes, all details had therefore to be made out from the complete series of transverse sections of *A australis*.

The cerebral flexure has almost disappeared, the axis of the prenasal region being very nearly in the same straight line as the notochord. The parachordals have largely united beneath the notochord, but the latter still comes to the surface of the basis cranii. The auditory capsules have nearly attained their adult form, the floccular fossa (fig 126, *flc f*) is well developed, and a deep groove (figs. 125 and 143–145, *pn c*) has appeared on the outer face of the posterior region of the capsule, which, closed laterad by the squamosal, becomes in later stages a pneumatic cavity (*cf* figs 75 and 77, *pn c*).

Immediately caudad of the dorsum sellæ the parachordals separate in the middle line to form the posterior basicranial fontanelle, the notochord at the same time turning dorsad (figs 126 and 140, *p bcr fo*). At this level the alisphenoids (fig. 140, *Al.Sph*) are seen in section to be continuous with the parachordals, and the orbitonasal nerve (*Nv V<sup>1</sup>*) is seen passing through the cartilage to reach the external aperture of the tunnel-like orbitonasal foramen. Considerably less than 1 mm. cephalad of this point (fig. 139), the posterior basicranial fontanelle has come to an end by the formation of the transverse commissure *y* already seen in preceding stages. This commissure (fig. 139, *y*) unites the parachordals some distance dorsad of their

ventral edge, so that these latter project as a pair of nearly parallel ridges (figs 124 and 139, *r*) which bound the posterior basicranial fontanelle on either side, and disappear anteriorly at about the level of the carotid foramina (fig 138, *Int car*), *i e*, just caudad of the basipterygoid processes

Immediately above the commissure *y* is the fibrous tissue forming the middle of the dorsum sellæ and containing the nodular prochordal cartilage (figs 126 and 139, *Pr Ch*), the distinctness of which both from the parachordal (*y*, *r*) and trabecular regions of the skull is perfectly clear

The middle basicranial fontanelle has disappeared by the concrescence of the commissures *x* and *y* (fig 126, *x*, *y*), the anterior fontanelle (*abc fo*) is, however, still present, its general direction being a little forwards from the pituitary fossa as well as downwards, so that the aperture by which it opens on the ventral surface of the skull is just cephalad of the vertical posterior border of the presphenoid (figs 134 and 135). The pedicle of evagination of the pituitary body (*pty. ped.*) can be traced from the fontanelle forwards and downwards to the mouth, perforating in its course the parasphenoidal rostrum (fig 134, *Rost.*); the fontanelle itself is covered by the stroma into which the ossification of the rostrum subsequently extends.

The alisphenoid (*Al Sph*) has the usual relations, it passes below into the trabecular and parachordal regions, and extends nearly as far forwards as the optic foramen (*Nv II*), lying, in the anterior part of its course, outside the orbitosphenoid (figs 137–139). It is perforated in the usual way by the fifth nerve.

The presphenoid (*Pr Sph*) is still nearly as long antero-posteriorly as in the three previous stages, but the orbito-sphenoids (*Orb Sph*) have undergone a marked reduction. Posteriorly they form nearly vertical plates bounding the optic foramina above (fig. 136), further forward they lie one on either side of the presphenoid, their point of origin being considerably below its dorsal edge (fig. 135), but gradually rising until in their anterior region (fig 133), they form lateral offshoots of the dorsal border of the presphenoid as in previous stages, but greatly diminished in width. A comparison of figs 105, 123, and 75 shows very clearly how the large orbitosphenoid of Stage F becomes a mere band of cartilage in the ripe embryo.

The mesethmoid (*M Eth.*) has a rounded, rod-like, lower border, its middle portion is narrow from side to side, while dorsad it expands again as it passes into the ectoethmoids, so as to be sub-triangular in section (figs. 131, 132). It presents one peculiarity not met with in any other stage, at the level of the anterior accessory turbinal (fig 132, *A A. Trb.*), and of the posterior nares (*Pt. Nu*) it contains near its upper border a small rounded cavity filled with connective tissue (*cr. fa. c.*), about 0.25 mm. in diameter, and probably, since it extends through rather more than 20 sections, nearly 0.5 mm from before backwards. I am disposed to consider this vacuity as probably homologous with the cranio-facial notch of the Chick (31, Plate 83, fig. 4, *cfe*), I cannot be sure, from my Father's description, whether it corresponds with the fenestria figured by BLANCHARD (*ante*, p 48).

The ectoethmoids (*Ec Eth*) have attained their full development, except that chondrification is still incomplete anteriorly (fig 129) even the small forwardly-directed process of the fifth portion (fig 124, *a*) is already well formed. The turbinals are also fully developed, and all but the naso-turbinal (fig 129, *Na.Trb*) are chondrified the latter, as also the anterior portion of the ectoethmoid, has not even reached the grade of prochondral tissue, but is indicated only by a concentration of nuclei in the mesoblast. Owing to the length of the presphenoidal region the posterior wall of the olfactory chamber or antorbital plate (see p 48) does not reach backwards to the optic foramen as in later stages. The external nostril and the anterior part (about 4 or 5 mm) of the nasal chamber are still filled with a solid mass of epithelial cells (fig 128)

The rudiment of JACOBSON'S cartilage (fig 132, *Ja C'*) appears as a somewhat ill-defined area of prochondral tissue extending through nearly forty sections, and, therefore, probably not more than 1 mm. in length.

The quadrate has the outer side of its head in close proximity to the squamosal (fig 142, *Qu., Sq*), but no articular cavity is yet developed for its reception on the latter bone. The cartilaginous mandible—MECKEL'S cartilage (*Mck C*) with its articular expansion (*Art*)—and the columella (*Col.*) have undergone no change of importance, and there is still no trace of the hyoid cartilage beyond a slight concentration of nuclei in the mesoblast of the end of tongue (fig 132, *C.Hy.*)

The position and extent of the membrane bones were accurately determined from serial sections, so that figs 120, 121, and 122, although restorations, are far more reliable than drawings of actual dissections would have been in the present very early condition of the bones. In the sections the bones appear as extremely delicate shining spicules, unstained by carmine although the head was not decalcified they were not sufficiently advanced to turn the edge of the razor

The premaxillæ (*Pmx*) appear in the 34th section, *i.e.*, about 0.5 mm. from the end of the beak, as paired deposits of bone encircling the prenasal cartilage, and nearly meeting above (fig 127) a few sections further back they have completely united dorsad of the cartilage, and in the 76th section the arch thus formed has divided into a median dorsal and paired lateral deposits, the rudiments respectively of the nasal and palatine processes (fig. 129) It is worthy of notice that even in this early stage there is no indication of the nasal process being double. The extent of the premaxilla is shown in figures 120–122 it reaches only about half-way along the beak

The maxilla begins immediately caudad of the premaxilla, and already shows its characteristic division into palatine and jugal processes. The jugal (*Ju*) and quadrato-jugal (*Qu.Ju.*) are delicate styles of bone, and the latter shows no indication of the cartilaginous facet by which in later stages it articulates with the quadrate (fig. 136)

The vomer (*Vo*) is Y-shaped, and its forwardly-directed stem has nothing to indicate a paired origin. The palatine (*Pal.*) is a simple rod, the pterygoid (*Ptg.*) is

forked, and for some distance caudad of the union of its mesial and lateral processes is triradiate in section (fig 133) · further back it becomes a slender rod (fig. 136), and abuts against the basipterygoid process (*B.ptg pr*) and the quadrate (*Qu.*). it shows at present neither of the cartilaginous articular facets present in the adult.

The rostrum or anterior division of the parasphenoid (*Rost.*) begins a short distance cephalad of the vomer, and ends just in front of the anterior basicranial fontanelle (fig. 134) it is, however continued backwards beyond the fontanelle by a band of dense mesoblast into which ossification subsequently extends. As already mentioned (p. 64) it is perforated a short distance in front of the anterior basicranial fontanelle by the pedicle of evagination of the pituitary body (*Pty ped*). There is no indication of the basitemporals or posterior division of the parasphenoid.

The frontal (*Fr.*) is of considerable extent but very thin its lower edge is turned in forming an orbital process, but there is, so far, no trace of the remaining processes of the adult bone. Its anterior border is continued forwards for a considerable distance (more than 100 sections, about 2 mm) by thick fibrous stroma, into which ossification subsequently extends. There is no trace of the parietal, which is thus very late in making its appearance. The squamosal (*Sq.*), on the other hand, is well developed, and is the thickest of all the bones at the present stage: there is, so far, no development of cartilage where it comes into contact with the head of the quadrate (fig 142).

The nasals (*Na.*) are paired patches of bone on the dorsal surface of the ectoethmoids at the junction of their third and fourth portions. Like the frontal the actual bone is continued some distance, both forwards and backwards, by a thick stroma, into which ossification afterwards extends. The lacrymals (*Lac.*) are small concavo-convex deposits, lying just mesiad of the lacrymal ducts.

The dentary (*Dent.*) begins a short distance cephalad of the anterior end of MECKEL'S cartilage (fig 129) and very soon divides into dorsal and ventral bars, which, after the appearance of the cartilage (fig 130) lie respectively dorso-laterad and ventro-mesiad of it, but gradually take up the first a lateral, the second a ventral position. The entire bone extends backwards about two-fifths of the length of MECKEL'S cartilage, and is continued caudad for a considerable distance by unossified stroma.

The splenial (*Spl.*) begins a short distance caudad of the posterior end of the dentary, and is about half the length of that bone. Both angular (*Ang.*) and supra-angular (*S.Ang*) commence a little in front of the posterior end of the splenial and extend back to the articular expansion of MECKEL'S cartilage. The coronary (*Cor.*) is a slender style situated just in front of the articular expansion.

*Stage H* (Plates 12-14, figs. 146-171).

In this stage the cartilage bones have appeared; all the membrane bones are present, *v.e.*, the parietals (*Pa.*) and basitemporals (*B.Tmp.*), in addition to those

developed in the previous stage, and the skull has, in all essential respects, apart from ankylosis, attained its final form. As shown in fig 146 (Plate 12), the main difference between the skull at this stage and that of the ripe embryo is the presence of a large fontanelle on the roof of the brain-case, due to the limited extent of the parietals and frontals. There is thus a very considerable gap between stages G and H, and certain points in the history of the skull, and especially of the basisphenoidal region, can only be finally settled by the examination of intermediate stages.

The form of the chondrocranium (fig 147) differs from that of the ripe embryo only in the more rounded contours of the auditory capsule. It will, therefore, be unnecessary to describe it in detail, except in so far as it is modified by the appearance of the cartilage bones and of the basitemporals.

The basioccipital (*B Oc*) is a lanceolate bone surrounding the notochord, and shown by sections (figs 168-170) to consist of tolerably dense inner (dorsal) and outer (ventral) plates, apparently ectosteal, united by bone of looser texture around the notochord. The exoccipitals (*Ex Oc*) are also double, their inner and outer laminae being continuous round the lateral border of the foramen magnum, as well as round the condyloid foramen (fig. 171). The supraoccipital has not appeared in one of the specimens belonging to this stage (*A bulleri*, fig 147), in the other (*A oweni*) it is present as an impaired ectosteal deposit consisting of outer and inner laminae. There is no indication of its being formed of paired osteites, as in the Chick (31, Plate 82, fig. 8).

The prootic (*Pr Ot.*) is a small irregular bone on the inner face of the anterior region of the auditory capsule. It is ectosteal and penetrates for a very short distance into the cartilage (fig 169). The opisthotic (fig 171, *Op.Ot*) is a small endostosis in the postero-ventral region of the auditory capsule, immediately mesiad of the utriculus and laterad of the exoccipital. There is no indication of a separate epiotic, but it appears to be already fused with the supraoccipital, since the latter bone is traceable on each side into the auditory capsule as far as the posterior semicircular canal.

The interpretation of the basisphenoidal region is made difficult by three changes which have occurred simultaneously since the previous stage. The parosteal basitemporals and the endosteal basisphenoid have made their appearance. These two bones have partly ankylosed, and the cartilage of the region has undergone partial absorption.

In the entire chondrocranium the basisphenoid (fig 147, *B Sph.*) appears in a view from above as an irregular bone forming the floor of the pituitary fossa and the dorsum sellae, and ending caudad immediately in front of the posterior basiscranial fontanelle (*p bcr fo*), which separates it from the basioccipital. A ventral view (fig 148) shows the basitemporals (*B Tmp*) already united with one another and with the rostrum. Their posterior edge is deeply notched, and between the notch



and the basioccipital lies the posterior basicranial fontanelle (*bp.crf.*) filled with connective tissue.

A transverse section through the posterior basicranial fontanelle (Plate 14, fig. 167) shows the cartilage of this region to be hardly at all absorbed, and to consist of paired halves, each with a broad ventral portion bounding the fontanelle (*p.bcrfo.*) and of a narrow dorsal portion inclined outwards. The basitemporals (*B.Tmp.*) are seen as paired parostoses lying ventrad of the cartilage, passing upwards into the fontanelle and partially ossifying the cartilage on each side. The lateral extension of the basitemporals beyond the cartilage is noteworthy as accounting for the increased breadth of the fully ossified skull in this region (*cf.* Plate 9, fig. 76, with Plate 11, fig. 124), and for the altered position of the carotid foramina, the arteries becoming enclosed between the basitemporals and the cartilage (*cf.* figs. 140 and 167, *Int.Car.*).

The section shown in fig. 166 is taken through the dorsum sellæ, and may therefore be considered as corresponding with fig. 139 (Plate 12) of the previous stage and with fig. 118 (Plate 10) of Stage F. The basitemporals have extended dorsad on each side, so as to come in contact with the basisphenoidal cartilage at its junction with the alisphenoids (*Al.Sph.*). A considerable space is thus shut in on each side of the primitive basis cranii, enclosing the internal carotid (*Int.Car.*) completely and the Eustachian tube (*Eus.T.*) partly. A large cavity (*pn.c.*) is also enclosed in the same space, filled at present with coagulum, but becoming in the adult the pneumatic cavity of the basis cranii. The section passes through the posterior end of the basisphenoid bone (*B.Sph.*), which extends downwards into the cartilage. The latter is largely absorbed, but the irregular area *Pr.Ch.* probably represents the prochordal cartilage, and the mass *y* the commissural band *y* of earlier stages (*cf.* fig. 139).

In the next section figured (fig. 165), which is also through the dorsum sellæ and not more than 0.1 mm. cephalad of fig. 166, the absorption of cartilage has gone farther still, mere traces of the medio-ventral region of the basisphenoid cartilage being left.

The three next sections (figs. 164, 163, and 162) are taken at short intervals between the dorsum sellæ and the pituitary body. In the hindmost (fig. 164) the depression for the pituitary fossa has already begun as far as the cartilage is concerned, but is bridged over by the basisphenoid bone (*B.Sph.*). Thus it would seem that one result of ossification is to fill up the hinder part of the pituitary fossa, and so to reduce slightly its antero-posterior extent (*cf.* Plate 10, fig. 111, and Plate 14, fig. 174).

In fig. 163 the internal carotids (*Int.Car.*) are seen emerging through their foramina into the pituitary fossa, so that this section corresponds fairly with fig. 138 (Plate 12) of Stage G. The cartilage is retained to a greater extent than in succeeding sections, there being a small ventro-lateral patch, which in fig. 162 (Plate 13) is seen to pass into the root of the basiptyergoid process (*B.ptg.pr.*) In both fig. 162 and fig. 163 the distinction between the basitemporal and the basi-

sphenoid is well marked ventrally, there being a distinct space between the two. Laterally, however, they pass into one another, and it would require a careful examination of one or more earlier stages to determine exactly their respective limits. As far as I can judge from the whole series of sections of the present stage, the colouring in figs 161-167 is correct.

Fig. 161 passes through the pituitary body (*Pty*) and the anterior basicranial fontanelle (*a bcr fo*). The basitemporal covers the fontanelle and is continuous on each side with the basisphenoid, which has here the form of paired ossifications in the cartilage, extending ventro-laterad into the basipterygoid processes.

At the level of the optic chiasma (fig 160, *Nv II*) the basisphenoid cartilage is quite unossified, and is underlaid by the rostral portion of the parasphenoid (*Rost*), which shows no tendency to invade the cartilage either here or elsewhere.

It appears, therefore, that the basisphenoid bone, in this stage, is an unpaired ossification in the medio-ventral region of the pituitary fossa, extending upwards or backwards into the dorsum sellæ, and sending forward paired prolongations on each side of the anterior basicranial fontanelle, that the basitemporal is a flat bone applied to the basisphenoid and curved upwards on each side so as to abut against the chondrocranium at the junction of the basi- with the alisphenoids and enclose paired spaces, external to the chondrocranium but mesiad of the basitemporal, containing the internal carotids and the pneumatic cavities of the skull floor, and that the basitemporal and basisphenoid have already largely ankylosed. In this way the form of the basisphenoidal region is profoundly altered by ossification.

Moreover, a glance at the sections shows that the pituitary fossa is much shallower, and the whole of this region of the skull more depressed, in this than in the preceding stage. Compare particularly fig 161 with fig 136, fig 163 with fig 138, fig 166 with fig 139, and fig 167 with fig 140.

The alisphenoid (fig 165, *Al Sph*) is ossified by a double ectosteal deposit. The presphenoid (fig 159, *Pr Sph.*) and orbitosphenoids are unossified, but the latter, reduced as already mentioned to a narrow band (fig. 147, *Orb.Sph*), is overlaid by the orbitosphenoid process of the frontal (fig 159, *Fr*).

An endostosis has made its appearance in the mesethmoid (figs 156, 157, *Eth Pr.Sph.*), but in the specimen of *A bulleri* it does not extend to the dorsal border of the cartilage, and is therefore not visible from outside (figs 146, 147). The turbinals are quite unossified, but the anterior portions of these and of the lateral ethmoids are now fully chondrified (figs 149-159). The anterior part of the nasal cavity as far back as the junction of the first and second portions of the ectoethmoid is still filled with a solid mass of epithelial cells (figs. 150-152).

The relations of the antrum of HIGHMORE are well seen in this stage. It is a spacious cavity (fig 158, *Ant.Hgh*) containing coagulum, lying ventro-laterad of the posterior portion of the ectoethmoid (*Ec Eth* 5) and below the orbit. Its posterior limit is at about the level of the hinder boundary of the eye in front



it divides into two branches, one of which (fig. 156, *Ant Hgh'*) enters the cavity of the anterior accessory turbinal (*A.A Trb.*), while the other (*Ant.Hgh''*) passes forward just outside the vential region of the ectoethmoid (*Ec Eth 4*) and soon ends blindly. I was not able to make out any connection between the antrum and the olfactory cavity.

The body of the quadrate (Plate 14, fig. 165, *Qu.*) is well ossified, but its articular ends (figs 165 and 169) and orbital process (fig. 160) are still cartilaginous. The otic process has its adult relations, articulating with the prootic, the alisphenoid, and the cartilaginous facet of the squamosal (fig 169). The articular (fig. 165, *Art*) is not yet ossified.

The membrane bones have advanced so far that there is nothing to add to the description of Stage K, except to mention that the dentaries and splenials have not yet ankylosed.

*Stage I* (Plate 14, figs. 172–174).

The advance beyond the previous stage is slight, the most important differences being due to the extension of the cartilage bones. The supraoccipital (fig. 172, *S.Oc.*) is well ossified. the ethmo-presphenoid (*Eth.Pr.Sph.*) has appeared on the surface, and extends both into the ectoethmoids and into the anterior half of the crista galli. All the other cartilage bones have increased in size so as to reduce the width of the synchondroses, and the great fontanelle in the roof of the skull has also diminished considerably.

In two of the specimens belonging to this stage sagittal sections of the basis cranii were made: these are shown in figs. 173 and 174, and illustrate certain points in the structure of this region of the skull with great clearness.

In both sections the basioccipital (*B.Oc.*) is seen to end at the hinder boundary of the posterior basicranial fontanelle (*p.bcr.fo*), the ventral lamina of the bone extending further forwards than its dorsal lamina. The notochord (*Nch.*) emerging from between the two laminæ, turns upwards and is traceable for some distance up the dorsum sellæ, being imbedded in the periosteum of the latter, and in the connective tissue of the posterior basicranial fontanelle.

In one of the two specimens examined (*A. australis*, fig. 173) a considerable portion of the cartilage of the basisphenoidal region is retained. The median portion of the dorsum sellæ is formed by a large cartilage (*Pr.Ch.*) apparently derived from the prochordal cartilage of earlier stages (Plate 11, fig. 126, *Pr.Ch.*). There is also a large irregular mass of unabsorbed cartilage (*xy*) in the floor of the pituitary fossa, evidently the remains of the commissure marked *xy* in Stage G (fig. 126). The basisphenoid bone (*B Sph*) is a thin plate continuous behind with the basitemporal (*B.Tmp.*).

In the other specimen (*A. bulleri*, fig 174) the basisphenoidal cartilage is completely absorbed and there is no trace of the prochordal nodule. The basisphenoid

bone (*B.Sph*) is continuous with the basitemporal both in front and behind, the posterior ankylosis being immediately cephalad of the posterior basicranial fontanelle (*p.bcr fo*), the anterior immediately caudad of the anterior fontanelle (*a.bcr fo*.)

*c. Changes Undergone by the Skull subsequent to Hatching*

*Stage L*

In a specimen of *Apteryx australis* a few weeks old the skull is considerably thicker and firmer than at the time of hatching. The intervals between the roofing bones are less than in Stage K, but their edges are still connected by membrane, there being no true sutures.

*Stage M*

In the dried skeleton of a young *A. owenii* the various cranial bones are still separate but in close contact with one another, the synchondroses between the cartilage bones being reduced to a minimum, and the roofing bones articulating with one another by true dentated sutures. The ethmo-presphenoid, although larger than in previous stages, has not yet extended into the presphenoid region, which is still cartilaginous. The turbinals had unfortunately been removed in preparing the skull: they were probably not yet ossified.

*Stage N*

This stage consists of the dried skull of a young specimen of *A. owenii*. Ankylosis has taken place between the occipital and otic bones and the basi- and ali-sphenoids. The lambdoidal suture is obliterated, but the coronal, sagittal, and frontal sutures still remain, as well as those between the frontals and alisphenoids.

The ethmo-presphenoid bone has extended so as to ossify the presphenoid, nearly the whole of the fifth or posterior portion of the ectoethmoid, the roof of the third and fourth portions, and the greater part of the turbinals. In the mesethmoid it has extended as far forward as the anterior end of the parasphenoidal rostrum. The bony ectoethmoids are still separate from the mesethmoid both ventrad and caudad, but the ethmo-presphenoid has already ankylosed both with the rostrum and with the orbitosphenoid processes of the frontals.

*Stage O.*

In two sub-adult skulls of *A. owenii* the sagittal, coronal, frontal, and fronto-ali-sphenoidal sutures are retained. The ectoethmoidal portion of the ethmo-presphenoid bone has further extended and has ankylosed with the perpendicular plate (mesethmoid *plus* presphenoid), the basisphenoid, and the descending process of the frontal. The lacrymal and the descending process of the nasal are still distinct, and

the sutures between the premaxillæ, maxillæ, palatines, pterygoids, and vomer are open

*Adult.*

In the adult skull the sutures in the brain case have completely disappeared the nasals have ankylosed with the nasal processes of the premaxillæ, with one another, and with the ethmo-presphenoid the lacrymal has united with the ectoethmoid and with the descending process of the nasal, and the palatine processes of the premaxillæ, the maxillæ, jugals, quadrato-jugals, vomer, palatines, and pterygoids, are all immovably united together Thus the quadrate and the columella are the only free bones in the skull Owing, however, to the slenderness of the connection between the nasal and palatine processes of the premaxillæ, and to the fact that the bones of the palate remain free from those of the base of the skull, the whole palate (*i.e.*, the united palatine processes of the premaxillæ, maxillæ, jugals, quadrato-jugals, palatines, pterygoids, and vomer) can be lifted away from the skull proper, the slender body of the premaxillæ serving as a hinge

## 2. THE VERTEBRAL COLUMN, INCLUDING THE RIBS.

### *a At the time of Hatching (Stage K).*

(Plate 15, figs. 175-190.)

The detailed descriptions of the vertebral column in the adult given by OWEN (24) and by MIVART (21) allow me to confine myself to such points of structure as can only be made out by the examination of young specimens

For descriptive purposes I find it necessary to make a slight addition to the terminology of this part of the skeleton. As BAUR (4) has pointed out, the so-called neurapophyses and pleurapophyses are not processes of the body but distinct elements, and he, therefore, proposes to call them respectively neuroids and pleuroids. He does not state, however, whether these terms are intended to apply to the cartilaginous or to the bony vertebræ or to both The distinction is an important one because the ossifications which appear in the neuroids extend ventrad into the centrum, so that the cartilaginous and bony elements of the vertebra do not strictly correspond one with another. In practice I find it very convenient to be able to state without unnecessary circumlocution, not only whether a given process springs from centrum or neuroid, but whether it is connected with the ossification of the centrum or with the ossification of the neuroid.

Starting with the terms chondrite and osteite already proposed (p. 43), the cartilages of which any vertebral segment is formed will be called respectively the *centrochondrite*, *neurochondrites*, and *pleurochondrites*. By the concrescence of

these is formed a cartilaginous vertebra, the regions of which are centrum, neuroids, and pleuroids. When ossification takes place one or two centres appear in the body, the *centrosteites*, one in each neuroid, the *neurosteites*, which extend ventrad into the body, and one in each pleuroid, the *pleurosteites*. Thus the entire centrum of the bony vertebra, although co-extensive with that of its cartilaginous predecessor, consists not only of the single or paired centrosteites but of the ventral ends of the neurosteites.

The atlas of a newly-hatched KIWĪ (Plate 15, figs. 175 and 176) consists of three distinct osteites, united by synchondrosis. As is proved by the development of the bone (p. 79), the ossification which forms the ventral portion, or so-called body (*pt oc int c*), is not the centrosteite but a postoccipital intercentrum. It is semi-lunar in form, having a concave dorsal and a convex ventral border; its anterior face is concave, its posterior face convex, and both are thinly covered with cartilage.

The neurosteites (*n ost*) are separated from the intercentrum by broad cartilaginous intervals, and meet with one another in the middle dorsal line by a very narrow synchondrosis. Between the dorsal border of the "body" and the broad cartilaginous ventral ends of the neuroids is a nearly semi-circular notch, across which is stretched a strong transverse ligament (*lg*) perforated in the centre for the odontoid. In this stage, therefore, the atlas has quite as obvious a dorsal notch as that of the other Ratitæ (*cf* MIVART, 21, p. 34). There is no trace of the hyp-apophysis present in the adult, and the hyperapophyses are small.

The axis (figs. 177–179) contains altogether seven ossifications—three in the compound body, one in each neuroid, and one in each pleuroid or transverse process.

The centrosteite of the axis itself (*c ost*) forms rather more than the posterior half of the body; it is flat in front, and presents behind the usual saddle-shaped surface covered by cartilage, in which a slight dimple marks the position of the notochord. Immediately cephalad of the dorsal half of this bone is the separate ossification of the odontoid (*Od*), which as BAUR has shown in Carinatae, and as will also appear from the consideration of earlier stages (p. 79) is really the centrosteite of the atlas. The odontoid is far less aberrant than in the adult (21, p. 34), being short and blunt with a flat dorsal and a convex ventral surface.

The third ossification of the body (*pt atl int c*) lies beneath the odontoid and cephalad of the ventral half of the true centrum, it is a transversely elongated bone with a concave anterior surface. It represents a second or post-atlantal intercentrum.

The neurosteites are united above by a thick mass of cartilage produced into a short blunt neural spine. The perforated transverse processes or pleuroids contain each a small pleurosteite (*pl.ost.*) at its ventral end; this is the "small and rudimentary parapophysial process" of MIVART.

The 3rd to the 15th vertebræ (figs. 180–182) resemble one another in essentials, in matters of detail there is nothing to add to MIVART's description.

Each contains five ossifications, a centriosteite (*cost*) forming the greater part of the body, paired neurosteites (*n.ost*), ossifying the neuroids and the dorso-lateral portions of the body, and paired pleurosteites (*pl.ost*), ossifying the ventral portions of the pleuroids.

The neuro-central suture (*n.c.su*) is somewhat oblique from before backwards, being lower at its anterior than at its posterior end, as a consequence, a smaller proportion of the body is formed from the neurosteites behind than in front (*cf* figs 181 and 182).

The most striking difference of the cervical vertebræ in this stage from those of the adult is their relatively smaller antero-posterior dimensions. This is well seen by comparing fig. 180 with MIVART'S woodcut (21, fig. 34, p. 36) of the corresponding vertebra in the adult.

The 16th (fig. 183) is the last cervical vertebra, according to HUXLEY'S notation, the first dorsal (thoracic) of OWEN, and the cervico-dorsal (better cervico-thoracic) of MIVART. It differs from its predecessors mainly in the large size of its pleurosteites (*Cv.Th.Rb*), which form slender free ribs about three-fourths the length of the vertebral ribs of the succeeding segment. MIVART does not specially describe the articulation of these ribs. OWEN (24, p. 33) states that "the part corresponding to the head and neck, as usual, is not developed, and it is attached to the transverse process by the part analogous to the tubercle." From this it would follow that in OWEN'S specimen there was no space corresponding to the vertebrarterial canal of the preceding vertebræ.

In the specimen now under discussion there are large cartilaginous parapophyses (*parap*) springing from the centrum and large cartilaginous downgrowths from the ventral surfaces of the transverse processes or diapophyses (*diap*). The head of the rib is single, but bears two distinct facets, nearly confluent on the left side, a tubercular facet articulating with the diapophysis and a capitular facet with the parapophysis. Between the two is a well-marked vertebrarterial canal.

The so-called uncinæ processes are distinct cartilaginous plates, attached by fibrous tissue to the posterior border of the ribs, and each containing a small endostosis. As they are not processes of the ribs at all, but independent chondrites, I propose to call them simply *uncinates* \*. In OWEN'S specimen they were absent in the cervico-thoracic vertebra.

In the 17th or first thoracic vertebra (fig. 184) the head (*capit.*) of the rib is quite short, and the tubercle (*tuberc.*) articulates with a thick cushion of cartilage

\* FÜRBRINGER states (11, p. 632) that uncinæ have not hitherto been found in *Dinornis*. This is certainly not the case; they have obviously not been described, since it is hardly likely that even the most insignificant paper on the subject can have escaped the learned author of the 'Morphologie und Systematik der Vogel', but they are by no means uncommon in deposits of Moa bones, and are present in no fewer than eight skeletons in the Otago University Museum, usually as distinct bones, but in some cases ankylosed to the ribs.

on the under side of the transverse process (*diap*). In the second thoracic (fig 185) this cartilage is reduced in thickness, and at the same time the head of the rib is lengthened. Thus, in passing from the cervical to the thoracic region, there is a gradual ascent of the plane of segmentation between the diapophysis and the tubercle of the rib

The first four thoracic vertebræ (17th to 20th of the whole series) bear ribs united to the sternum by ossified sternal ribs (see fig. 204), the next four (21st to 24th) have few ribs, and are called by MIVART dorso-lumbar. This name appears to me an unfortunate one, a lumbar vertebra is defined as one devoid of ribs, so that these vertebræ are in no sense transitional between the thoracic and lumbar regions.

The first six thoracic ribs bear uncinates (see fig 204, *Unc*), in the seventh and eighth these bones are absent. This is also the case in OWEN'S figure (24, Plates 8 and 9), but it is stated in the text that they are present in all but the last

The last thoracic (24th) vertebra (figs 186 and 187, *Th.* 8) shows transitional characters between the remaining thoracic and the lumbar vertebræ. The diapophysis (*diap*) is short and confluent at its base with the parapophysis, and the capitular and tubercular facets of its ribs are also confluent.

In one of the specimens belonging to this stage, a newly-hatched *A. australis*, the last thoracic is already united to the first lumbar by the concrescence of their centrochondrites (figs 186 and 187), their centrosteites are, however, quite distinct, and the only union between the arches takes the form of a narrow longitudinal bridge of cartilage from spine to spine. In an unhatched *A. bulleri* the last thoracic is still free

The twelve vertebræ following the last thoracic—viz, the 25th to the 36th of the entire series—are united together by complete concrescence of their centrochondrites, and partial concrescence of their arches, by median longitudinal bands uniting the unossified neural spines (fig. 186). Both centrosteites and neurosteites are still quite distinct, and the ilia can be readily removed by maceration, so that there is no difficulty in determining the precise number and character of the vertebræ comprised in the compound sacrum, or, as it may conveniently be termed, *syn-sacrum*. As there is some difference of opinion as to the interpretation of this difficult region, I propose, in the first instance, to describe the facts as I find them in the specimens now under discussion, and afterwards to give the conclusions at which I have arrived as to the classification of the several vertebræ.

In the 26th to the 33rd vertebræ the ventral face of the centrum undergoes a marked flattening, and, as a consequence, the neuro-central suture or synchondrosis is lowered in position (fig 186). This is especially the case in the 28th vertebra,\* in which the centrosteite can barely be seen from the side. At the same time the

\* In figs 186–190, the number in brackets is that of the vertebræ in the entire series. e.g., the first caudal is marked *Cd* 1 (30)



neural canal is greatly increased in vertical extent, to accommodate the sacral enlargement of the myelon.

In the majority of the vertebræ of the syn-sacrum—namely, from the 23rd to the 33rd—the intervertebral foramina (fig 186, *int vert for.*) are vertical slits between the vential ends of the neurosteites

The 25th vertebra (*Lb. 1*) resembles the 24th or last thoracic, but its transverse process is smaller, and consists of a low oblique ridge arising entirely from the neurosteite. In the 26th the transverse process is still blunter, and shows a tendency to divide into two parts, a parapophysis (*parap*) arising partly from the neuro-central synchondrosis, and a very low roughened elevation (*diap.*) on the neurosteite, which represents the diapophysis.

In the 27th and 28th vertebræ the di- and pleur-apophysis are separate. The diapophysis is reduced to a roughened area on the neurosteite, hardly raised above the level of the bone, the pleurapophysis is a blunt process, arising entirely from the neuro-central synchondrosis, and, in the 28th vertebra, of considerable size (fig. 187, *Lb 4, parap.*).

In the next four (29th–32nd) vertebræ, there is no trace of parapophyses; in the 29th there is an inconspicuous diapophysial area on the neurosteite, similar to, but smaller than, those on the preceding vertebræ; in the 30th and 31st there is no trace of this area, these vertebræ being wholly without transverse processes; in the 32nd, although the parapophysis is still absent, the diapophysis is represented by a low cylindrical cartilaginous elevation, arising from the neuroid immediately above the neurosteite, and abutting against the ilium.

In the 33rd vertebra (*Sc. 1*) the diapophysis is like that of its predecessor, but the parapophysis is an outstanding process containing a distinct ossification, the pleurosteite or sacral rib (*pl.ost.*). In the 34th there is also a distinct pleurosteite, which is curved forwards so as to approach distad the corresponding part of the preceding vertebra, the cartilaginous ends of the two sacral ribs being united (fig. 187): the diapophysis and parapophysis are united by a vertical ridge of cartilage (fig. 186). In the 35th the di- and par-apophysis are also united by a vertical ridge, and the pleurosteite or sacral rib is short and free at its distal end (fig. 187).

The united ends of the first and second sacral ribs abut against the cartilaginous interval between the ilium and ischium, immediately caudad of the acetabulum and mesiad of the antitrochanter

The 36th vertebra (*Cd. 1*) has the centrum laterally compressed, and the transverse process is a vertical ridge representing both di- and par-apophysis. The neuro-central suture in this, and indeed in the two or three preceding vertebræ, is precisely at the junction of centrum and neuroid, so that, for the first time, the vertebral body consists entirely of the centrosteite, the neurosteites being confined to the arch.

According to HUXLEY's notation (16), the 25th to the 28th vertebræ are lumbar, the 29th to the 32nd sacral, while the 33rd to the 36th are the first four of the caudal

series MIVART (21), largely following GEGENBAUR, calls the 25th to the 28th lumbar, the 29th to the 32nd lumbo-sacral, the 33rd to the 35th sacral, and the 36th the first caudal. The two chief factors in determining the question are (1) the origin of the nerves which unite in the sacral plexus, and (2) the presence of distinct sacral ribs. HUXLEY lays the greatest stress on the first of these, both are taken into consideration by GEGENBAUR, as also by MIVART and CLARKE (22*a*), in whose paper the whole question is discussed. My Father (38) follows HUXLEY.

It appears to me that without a fairly complete series of the intermediate forms between Birds and their reptilian or proto-reptilian ancestors, the question is rather one of dialectic than of inductive morphology. After a careful consideration of the arguments, I have come to the conclusion that, in the present case at any rate, GEGENBAUR'S view has the most to be said for it, and that the vertebræ bearing distinct pleurosteites (33rd-35th) are those to which the name sacral should be applied. MIVART'S name, lumbo-sacral, for the presacral vertebræ without par-apophyses is convenient, and well worthy of adoption.

The 37th or second caudal is even more compressed than the first, and has no trace of transverse processes. The 38th is somewhat less compressed, and shows no distinction between centrosteites and neurosteites. Its arch bears a very inconspicuous diapophysial tubercle, and there is a distinct neural spine. It is the last vertebra with which the ilia are in contact, so that the syn-sacrum of *Apteryx* includes three thoracic, four lumbar, four lumbo-sacral, three sacral, and three caudal vertebræ.

The name sacro-caudal, applied to the first three caudal vertebræ by MIVART, although convenient in some respects, is hardly necessary. If, in the designation of the vertebræ, the fact of their union in the syn-sacrum is to be expressed, the last three thoracic should be called thoracico-sacral, and all the lumbar, lumbo-sacral. As already stated, I propose to retain the name lumbo-sacral for the 29th-32nd vertebræ, not to intimate their union in the sacrum, but to express the fact that they are vertebræ of a special character, coming between undoubted lumbar and probable sacral vertebræ.

The 39th or fourth caudal is the first free vertebra of the caudal series. It is considerably smaller than its predecessors, and its neural spine is so short as to be practically obsolete. In it also there is no distinction between centrosteites and neurosteites, the ossification of the body passing dorsad into the neuroids. There is a very short and inconspicuous diapophysis. The 40th differs from its predecessor in the possession of a short cartilaginous parapophysis (fig 187, *Cd* 5, *parap*) in addition to a very inconspicuous diapophysis.

In the 41st-43rd (6th to 8th caudal) the di- and par-apophyses have united into a blunt vertically elongated tubercle, which occupies the whole lateral surface of the centrum. The neuroids are united dorsad by connective tissue, so that the short neural spine is double (fig 189, *Cd* 8, *neur*).

In the 44th-46th (ninth to eleventh caudal) the neural canal is open above, the



neuroids being widely separated, and, indeed, in the 45th and 46th, slightly divergent (fig. 189). The 44th and 45th resemble their immediate predecessors in general form, but the 46th, or last vertebra of the entire series (figs 188 and 189, *Cd* 11) is a broad trough-like bone, somewhat resembling the pygostyle of many birds. The 45th and 46th differ from the seven preceding vertebræ in having distinct neurosteites (figs. 188 and 189, *nost*) in the form of minute endosteal granules in the short neuroids.

The vertebral formula of the specimen described may therefore be written thus —

$$Cv\ 15\ Cv\ Th\ 1\ Th.\ 4 + 1 + \overbrace{3\ Lb\ 4\ Lb\ Sc\ 4.\ Sc\ 3\ Cd.\ 3}^{S\ Sc.} + 8 = 46,$$

11

*i.e.*, there are fifteen cervical vertebræ, one cervico-thoracic, eight thoracic — of which the first five are free, and of these the first four have ribs articulating with the sternum — four lumbar, four lumbo-sacral, three sacral, and eleven caudal, of which the last eight are free. The bracket encloses all those vertebræ which are in contact with the ilia, and so form the syn-sacrum.

There are two caudal intercentra, each consisting of paired cartilages (*int.cent*), the first lying between the eighth and ninth caudal vertebræ, the second extending from the posterior end of the ninth to the anterior end of the eleventh.

In a ripe but unhatched chick of *A. bulleri* referable to this stage, the last thoracic has not yet united with the first lumbar vertebra, but the only differences of importance are in the caudal region, which contains (fig 190) only nine vertebræ, and a vestige of a tenth. The ninth (44th of the whole series) alone has an open arch, without neurosteites, and the tenth (*Cd.* 10) is a mere nodule of cartilage attached to the posterior face of the body of its predecessor. The specimen also serves to confirm the observation made above, that the neuroids of most of the caudal vertebræ are ossified by dorsal extensions of the centrosteite, or in other words, have each but a single centre of ossification.

### *b Development of the Vertebral Column.*

#### *Stages A and B (Plate 4, figs. 31–33)*

The secondary segmentation of the vertebral column has begun. The mesoblastic somites are still separated by narrow fissures (fig. 33, *f.*), the muscle plates (*M.Pl.*) are differentiated, and the mesoblast immediately surrounding the notochord is undergoing concentration to form the rudiments of the vertebral bodies (figs. 31–33, *Cent.*).

#### *Stage C (Plate 5, figs. 43 and 44).*

The patches of concentrated mesoblast from which the centra arise (fig. 44, *Cent.*) are considerably more obvious than in the preceding stage, and the cells composing them have become arranged in a concentric manner round the notochord (fig. 43, *Cent.*). They have not yet, however, passed into the condition of prochondral tissue.

*Stage D* (Plate 15, figs 191-193).

The vertebræ are now well chondrified, and in all cases the neuro- and centro-chondrites have united so as to form complete cartilaginous vertebræ. The neural arches are, however, incomplete dorsad throughout the whole column, the neuroids not having yet united above the spinal cord. This is particularly well marked in the sacral (fig 193) and caudal regions, in which the whole dorsal surface of the cord is covered only by membrane. In the sacral region, moreover, the right and left moieties of the centrum do not quite meet below the notochord (fig 193), so that the body presents a narrow membranous interval in the middle ventral line.

The pleurochondrites of the cervical vertebræ or cartilaginous cervical ribs (fig 191, *pl chn*) have evidently only recently chondrified, and form mere nodules united by membrane with the di- and par-apophyses. The thoracic ribs (fig 192) are well chondrified, but there is no trace of sacral ribs (fig 193), and in fact the whole of the post-thoracic vertebræ appear to be devoid both of lateral outgrowths and of pleuro-chondrites.

The vertebræ generally are very much higher in proportion to their breadth than in later stages, the centra being nearly circular in section and the transverse processes short (compare fig. 191 with fig 181, and fig 192 with fig 184).

*Stages E and F* (Plate 15, figs 194-197)

In both these stages the vertebral column was cut into sagittal sections, there is so little difference between them that they may be considered together.

The vertebral formula differs from that given on p 78 in the presence of an additional caudal vertebra, the total number being 47. The cartilaginous centra are still annular, the notochord having undergone but little relative reduction; its diameter is on the average more than half that of a centrum.

The composition of the atlas and axis is remarkably well seen, and corresponds precisely with BAUR's account (4). The true body (centrochondrite) of the axis (fig 194, *c chn.*) is similar to that of the succeeding vertebræ, but is joined in front by a narrow fibrous interval to the odontoid or atlantal centrochondrite (*Od.*), which like the other vertebral bodies and the basioccipital (*Oc.Cn.*) is perforated by the notochord. Lying together ventrad of the notochord are two intercentra, one post-occipital (*pt oc int c*) which forms the so-called body or inferior arch of the atlas, the other post-atlantal (*pt atl int.c*) which subsequently unites with the proper body of the axis behind and with the odontoid above. The neurochondrites of the atlas have already united with the post-occipital intercentrum but have not yet joined with one another above the spinal cord. In all the succeeding vertebræ the neural arches are completely formed.

The notochord as seen in a median longitudinal section of the cervical region (fig. 194, *Nch*) has straight dorsal and ventral contours, but sections taken a short distance to the right or left of the median plane (fig. 195) show it to be distinctly

beaded, being constricted in the middle of each centrum and dilated intervertebrally.

In the thoracico-lumbar region there are, in addition to the vertebral constrictions, slight constrictions of the notochord in the intervertebral regions, the rudiments of the menisci having grown inwards as narrow annular ridges. In the sacral (fig 196) and anterior caudal regions both vertebral and intervertebral constrictions are well marked, there being two notochordal "beads" to each vertebral segment. In the posterior caudal region (fig 197) the only constrictions on the dorsal surface are intervertebral, there being a distinct dilatation in each centrum; ventrally, however, there are vertebral ingrowths as well.

My Father (38) considers "these beadings as a true historical record of development," and as indicating a far greater number of vertebræ in the ancestors of Birds than in existing forms. I think, however, that a good deal of weight should be attached to the fact that the number of segments in *Apteryx* undergoes no alteration from a period corresponding to the fourth day of incubation in the Chick.

The last free and normal vertebra is the 45th (*Cd* 11); the body of the 46th (*Cd* 12) is fused ventrad of the notochord with that of the 47th (*Cd* 13), but is free above the notochord. The body of the 47th is a long hollow cone of cartilage, projecting some distance caudad of its arch, so that the posterior end of the neural canal is freely open above.

The uncinates (Plate 16, fig. 217, *Unc.*) are quite separate from the corresponding ribs, and are not chondrified.

#### *Stage G* (Plate 15, figs. 198–203).

In one specimen belonging to this stage (*A. oweni*) the vertebral column was prepared by dissection, and the vertebræ examined separately, in the other (*A. australis*) transverse sections were made.

The atlas (fig. 198), examined as an opaque object, appears to have an annular body, there being a complete foramen instead of a notch for the odontoid. Sections show, however, that the part lying dorsad of the odontoid foramen (*lg.*) is formed of indifferent tissue, and is the rudiment of the ligament (figs. 175 and 176, *lg.*) found in this position in later stages. The neural arch is still completed above by indifferent tissue.

In the axis (figs. 199 and 200) the three chondrites of the compound body have all coneresced, the vertebra now consisting of solid cartilage. The pleurochondrites (*pl chn*) are very small, and their dorsal or tubercular ends have united with the neuroids, their ventral or capitular ends being still separated from the centrum by a narrow tract of indifferent tissue. The odontoid (*Od.*) is a short nipple-like process, on the apex of which is a minute dimple (*Nch.*), indicating the position of the greatly reduced notochord.

There is nothing of special importance about the remaining cervical, the thoracic (fig. 201), or the lumbar vertebræ, except that all those going to form the syn-sacrum

are quite distinct, concrescence of the cartilaginous centra not having yet commenced. The sacral vertebræ (fig. 202) have diapophysis (*diap*) and parapophysis, or rather pleuroids (*pleur*), quite continuous respectively with neuroid and centrum, so that transverse sections of earlier stages would be required to show whether or not the sacral ribs originate as distinct chondrites.

There are twelve caudal vertebræ, the last of which, or 48th of the whole series (fig. 203), is short and nodular. Comparing the end of the tail in this and other stages, it would appear that, in the present case, an additional centrum is differentiated from the cartilaginous sheath of the caudal end of the notochord, the 47th and 48th vertebræ of the embryo now under discussion having the same general relations as the elongated 47th of Stage E (fig. 197), or of the trough-like 46th of the ripe embryo (fig. 189). It is quite obvious that the precise mode of segmentation of this region is a matter of individual variation.

In the last three vertebræ (fig. 203), the neuroids do not meet in the middle dorsal line, the neural arch being, therefore, widely open above. In the 45th, there is a fibrous union, in all the rest the neural arch is completed above by cartilage.

As to their general form the vertebræ are about intermediate between the high or compressed condition of Stage D, and the broad or depressed condition of the advanced embryo or adult (compare figs. 192, 201, and 185).

### Stage H

One of the specimens belonging to this stage (*A. oweni*) presents a peculiarity in the vertebral formula, which is

$$\begin{array}{ccccccccccc} & & & & & & & S & Sc & & \\ Cv & 15 & Cv & Th & 1 & Th & \underbrace{4 + 1 + 2}_{7} & Lb & 4 & Lb & Sc & 3 & Sc & 3 & Cd & \underbrace{3 + 9}_{12} = 45, \end{array}$$

that is, there is one thoracic and one lumbo-sacral vertebra less than usual, while the number of free caudal vertebræ is nine. In the other specimen (*A. bulleri*) the numbers are normal.

The vertebræ have practically assumed their adult characters. Ossification has begun and concrescence of the cartilaginous bodies of the lumbar, lumbo-sacral, and sacral vertebræ has taken place.

In the atlas the neurosteites only have appeared, the body (post-occipital intercentrum) being still unossified. In the axis there is a centrosteite in the body proper and another in the odontoid, but no ossification has yet appeared in the antero-ventral region of the body, or post-atlantal intercentrum.

The remaining cervical and the anterior thoracic vertebræ have small centrosteites and neurosteites. From the posterior thoracic to the sacral region only centrosteites have made their appearance, the arches being still unossified. The caudal region is

wholly cartilaginous. The last caudal vertebra is conical and longitudinally grooved above, its neuroids being represented by mere low ridges which do not meet above the myelon.

The vertebral ribs are ossified, but their uncinate, as well as the cervical and sacral pleuroids, are still cartilaginous.

#### *Stage I* (Plate 15, fig 204)

This stage only differs from its predecessor in the further extension of ossification.

Fig. 204 is introduced in order to show the relations of the vertebral column, vertebral and sternal ribs, uncinate, sternum, shoulder-girdle, and pelvis in an advanced embryo. It will be seen that in the specimen figured there is no uncinate on the cervico-thoracic rib (*Cv Th Rb.*)

### *c The Vertebral Column subsequent to Hatching*

#### *Stage L*

This stage differs from the newly hatched embryo (Stage K) only in the further advance of ossification, the cartilage being now nearly replaced by bone. The various osteites are, however, distinct. The last three caudal vertebrae have open arches, and the last is scoop-shaped.

#### *Stage M.*

The centrosteites and neurosteites of each vertebra have ankylosed, but the pleurosteites of the cervical vertebrae remain distinct, and there is no union of the separate (bony) vertebrae in the sacral region. The atlas still consists of three bones, its neurosteites not having yet united with the post-occipital intercentrum and the odontoid and post-atlantal intercentrum have not yet ankylosed with the body of the axis.

The rib of the last thoracic vertebra is only 4 mm. long, and does not project beyond the ilium. If ankylosed to its vertebra the latter would certainly be counted as the first of the lumbar series. There are only three lumbar vertebrae, the lumbo-sacral are four, and the sacral three as usual, and there are twelve caudal, the last of which is a short blunt bone, its small neuroids meeting above.

#### *Stage O* (Plate 15, fig 205).

Of this stage I have only the syn-sacra of two sub-adult specimens of *A. oweni*. In both the number of lumbar vertebrae is four, but there are only three lumbo-sacral. Most of the vertebrae have completely ankylosed, only the last thoracic (*Th.* 8), third sacral, and first caudal (*Cd.* 1) remaining partly free. Ossification has extended between the roots of the spinal nerves, so that each intervertebral foramen (*int.vert.for.*) is now replaced by two small apertures, one for the dorsal and one for the ventral root of the nerve.

*Adult* (Plate 15, figs 206 and 207).

The number of cervical vertebræ appears to be quite constant, viz, fifteen the 16th vertebra is also, in all specimens which have come under my notice, a cervico-thoracic, i.e., bears free ribs which do not meet the sternum. In every instance but one these ribs are of considerable length—more than 30 mm—and reach within a short distance of the sternum, but in a skeleton of *A. australis* in the Otago University Museum they are only 12 mm long

In every skeleton examined, except one, the number of thoracic vertebræ is eight, the first four of which are connected with the sternum by sternal ribs, while the last three are covered by the ilia and so form part of the syn-sacrum, only the last being ankylosed. The single exception is in the skeleton of *A. australis* referred to in the preceding paragraph, in which the 25th vertebra—corresponding to the first lumbar in other cases—bears on the left side a short rib about 11.5 mm long, and must, therefore, be counted as a ninth thoracic.

The usual number both of lumbar and lumbo-sacral vertebræ is four, but in some instances there are four lumbar and three lumbo-sacral, in others three lumbar and four lumbo-sacral. The sacral vertebræ proper appear to be invariably three, and there is the same number of caudal vertebræ included in the syn-sacrum (sacro-caudal, MIVART). The single exception to this is in the case of a skeleton of *A. owenii* in the Museum, in which there are four vertebræ behind the third sacral within the limits of the syn-sacrum the first of these bears diapophyses as distinct as the ankylosed ribs of the third sacral, and may therefore be a true (fourth) sacral vertebra; the fourth is only partly covered by the ilia.

The number of vertebræ caudad of the syn-sacrum is also fairly constant in every skeleton examined, except one, there are six free vertebræ, followed by a pygostyle, which is obviously formed by the union of either two or three (figs 206 and 207, *Pyg*). The pygostyle is a conical bone, and, in every case examined, its neural canal was completely closed in above (fig 207), this process evidently taking place after hatching. In the skeleton of *A. owenii* referred to in the previous paragraph there are seven free caudal vertebræ, the last of the series being apparently single, so that in this case there is no pygostyle.

The total number of vertebræ and their distribution among the various regions may be expressed by a formula as follows —

$$\begin{array}{c}
 \text{Cv. 15} \quad \text{Cv. Th. 1: Th} \quad \overbrace{4+1+3(4 \text{ or } 2)}^{S \text{ Sc}} \quad \text{Lb. 4(3)} \quad \overbrace{\text{Lb Sc. 4(3)} \quad \text{Sc. 3}}^{Pyg.} \quad \overbrace{\text{Cd } 3(4)+6+3(2 \text{ or } 1)} \\
 \underbrace{\hspace{10em}}_{8(9 \text{ or } 7)} \hspace{10em} \underbrace{\hspace{10em}}_{12(13 \text{ or } 11)} \\
 = 47(46 \text{ or } 45),
 \end{array}$$

that is, there are fifteen true cervical vertebræ without free ribs; one cervico-thoracic bearing free ribs which do not meet the sternum; usually eight, but occasionally nine



or seven thoracic, of which the first five are not covered by the ilia, and the first four bear ribs meeting the sternum, four or sometimes three lumbar with distinct parapophyses, four or occasionally three lumbo-sacral without parapophyses, three sacral with autogenous parapophyses or pleurosteges; three or rarely four caudal covered by the ilia, and from seven to nine free caudal, of which the last three or two are usually ankylosed to form a pygostyle. The ilia are supported by about fourteen vertebræ, from the sixth thoracic to the third (rarely fourth) caudal, which therefore constitute the syn-sacrum. The total number of vertebræ is usually forty-seven, but may be forty-six or occasionally forty-five. There appear to be no constant differences between the species in the vertebral formula.

I have found caudal intercentra in one skeleton only (*A. australis*). they have the form of irregular nodules of bone (fig 206, *int.cent*), one between the pygostyle and the preceding (ninth) caudal vertebra, the other between the eighth and ninth.

The general rule appears to be, as MIVART states, that uncينات are present on the cervico-thoracic and on the first six thoracic ribs, but the short cervico-thoracic ribs of the skeleton of *A. australis* referred to above (p. 83) are devoid of those appendages, which are also absent on one side in another skeleton examined. OWEN also states that they are absent in the specimen first examined by him. The occasional absence of the cervico-thoracic uncينات, taken in connection with the vestigial condition of the ribs in one case, and with the fact that in the same skeleton the first thoracic rib of the right side terminates ventrad in a blunt free end and has no sternal portion, seems to point to an inclusion of anterior thoracic vertebræ in the cervical region by atrophy of their ribs.

### 3 THE STERNUM.

#### a. In the Adult.

(Plate 16, figs. 208–215.)

The descriptions of the sternum by OWEN (24, p. 34) and by my Father (43, p. 191)—the only two detailed accounts I have met with—give all the essential features of the bone, and at the same time serve to show its great variability. In OWEN's specimen (*A. australis*) the posterior lateral processes are slightly longer than the posterior median process, the anterior margin is deeply and evenly excavated, and there are two large perforations, one on each side of the middle line. In my Father's specimen, also stated to be *A. australis*, the posterior median is considerably longer than the posterior lateral processes, the anterior margin is sinuous and is produced in the middle line into a small projection, and there are no perforations.

Miss LINDSAY (19) gives outline figures of the sterna of *A. bulleri* (= *mantelli*) and *A. oweni*\*; both show an even anterior emargination—deepest in *A. bulleri*, no

\* These are erroneously stated to be one and a-half natural size they are really less than two-thirds.

fenestræ, and the posterior lateral rather longer than the posterior median process, which latter is bifid in *A. oweni*.

As far as I have been able to ascertain, no previous observer has called attention to any characters in the bone of specific importance. From the small series of skeletons which have come under my notice, certain points appear to be fairly constant. As one of these depends upon the relative length and breadth of the bone, it is necessary to define these terms.

Both posterior median and posterior lateral processes are tipped, in the fresh state, with cartilage (Plate 16, fig. 213), which is usually absent in the dried skeleton, so that the greatest length of the sternum, measured from the apex of the anterior lateral to the extremity of the posterior lateral process, is a variable quantity, depending upon the extent to which ossification has advanced. The same objection applies to taking the length from the middle of the anterior border to the posterior median process, since the latter varies in length with age.

A more constant dimension is, however, furnished by the length of the corpus sterni as measured from the centre of its anterior border to a point midway between the two posterior notches (*ab* in figs. 208, 212, and 214). This I call *length of corpus sterni*, by *breadth of corpus sterni* I understand the length of a straight line drawn transversely across the sternum at about the level of the facets for the second pair of sternal ribs (*cd* in the same figures).

In *A. australis* the length of the corpus sterni appears to be constantly more than half its breadth, and the anterior border is concave with an even curve (figs. 208 and 209).

In *A. bulleri* the length of the corpus sterni is—often considerably—less than half its breadth. The anterior border is more deeply emarginated than in *A. australis*, and presents an even curve. The anterior lateral processes are usually blunter than in *A. australis* (figs. 212 and 213).

In *A. oweni*, besides the smaller size of the entire bone, the length of the body is less than half its breadth. The emargination of the anterior border is about the same as in *A. australis*, but instead of being even it is slightly sinuous, each side presenting a sigmoid curvature (figs. 214 and 215).

In the supposed skeleton of *A. haastii* (p. 38) the length of the corpus sterni is much greater than its breadth, and the characters generally agree with those of *A. australis* (fig. 210).

As far as my own observations go, these characters are constant, but my Father's figure of the sternum of *A. australis* (43, Plate 17, fig. 1) shows an uneven anterior curvature with a slight median projection, and the length, as defined, is less than half the breadth, while in Miss LINDSAY'S figure of *A. oweni* (19, p. 712, fig. 5, 5) there is no trace of the sinuosity of the anterior border, and the length is a little more than half the breadth.\*

\* I am disposed to think that skeletons of *Apteryx* often bear wrong specific names. There ought



Trifling as these characters are, and inconstant as they may probably prove to be I think them worth giving as showing that the three or four species of *Apteryx* are tending to differentiation in their skeletons as well as in their external characters.

One point not yet referred to appears to be of considerable interest. As a general rule the costal borders of the bone are thick and strong, the thickening extending to a greater or less extent on to the anterior border, but the rest of the bone being thin and translucent. But in two specimens of *A. bulleri* (fig 213), in the doubtful *A. haastii* (fig 210), and in the skeleton in the Wellington Museum marked *A. maxima*, but probably referable to *A. bulleri* (fig. 211), the corpus sterni presents a distinct median longitudinal thickening (*k*) along its anterior half, the result being the production of a low ridge nearly as well marked as the vestigial keel of *Stringops*. In a skeleton of *A. australis* in the Canterbury Museum (fig 209), there is a very poorly developed ridge, which projects on the inner or dorsal surface of the bone instead of on the ventral or outer surface, as in all other cases.

On the hypothesis that the Ratitæ are descended from birds which possessed the power of flight, the occasional occurrence by reversion of a vestigial keel is precisely what might be expected. The absence of a special osteite (lophosteon) for the keel hardly appears to be of such fundamental importance as it is sometimes assumed to be. I should rather take the presence or absence of such a bone as a fact of the same rank as the presence or absence of a distinct centre of ossification in the spines of the thoracic vertebræ of mammals. But this is a point upon which the development of the sternum in *Stringops* should throw light.

In one skeleton of *A. australis* there is an exception to the usual rule that four sternal ribs are articulated to the sternum; on the left side the fifth thoracic rib is attached by a true joint, the articular cavity being on the proximal end of the posterior lateral process.

#### *b. Development of the Sternum.*

##### *Stage E* (Plate 16, fig 216).

In this the earliest stage in which the sternum was observed, owing to the damaged condition of Stage D, it consists of paired cartilaginous plates, there being no indication of the metasternum or posterior median portion.

Owing to the way in which the ventral body-wall was ruptured (Plate 3, fig. 6) the moieties of the sternum had a position nearly parallel to the median plane of the body, and are, therefore, well seen in sagittal sections. Each (fig. 216, *St.*) is roughly triangular, with a thickened anterior margin, to which the coracoid (*Cor.*) is articulated, and an extremely thin mesio-ventral border. The anterior edge is sinuous.

never, of course, to be any mistake about *A. oweni*, but the other two common species are very easily mistaken for one another.

The position of the sternum is remarkable, its antero-posterior axis is as nearly as possible parallel with that of the vertebral column, as in a Carinate Bird, instead of being nearly at right angles to it, as in the adult and advanced embryo (*cf.* figs. 204 and 216)

There are only three ribs attached to the costal border, and the third of these (*Th Rb 3*) appears to be united by indifferent tissue. The cervico-thoracic rib (*Cv Th Rb*) is separated by a wide interval from the sternum. There is thus a striking difference from many of the embryos investigated by Miss LINDSAY (19), in which the number of ribs attached to the sternum is greater in the embryo than in the adult. The joints between the vertebral and sternal ribs, and between the first two sternal ribs and the sternum, have already appeared. They are not shown in Miss LINDSAY's figures of even considerably later stages, but this is probably due to that observer not having corrected the results of her dissections by the subsequent examination of thin sections.

#### *Stage F* (Plate 16, fig. 217)

The two halves are still separated by a considerable interval, and there is no indication of the metasternal region. The coracoid grooves are very obvious in sections, and the sternum has extended caudad slightly beyond the ventral end of the fourth thoracic rib (*Th.Rb 4*). From a dissection of the specimen, it appeared that this rib was attached to the sternum, but sections show that it is really separated by a short but perfectly distinct interval.

Comparing this stage with the last, it appears certain that in *Apteryx* each half of the sternum is not formed by the antero-posterior union of the whole of the sternal ribs. In Stage E only two ribs are united by joints, and a third is loosely attached by indifferent tissue at the posterior boundary of the sternum. In Stage F the sternum has apparently grown backwards to the level of the fourth thoracic rib, which has extended mesiad to meet it.

As to position, the posterior end of the sternum is now at a considerably lower level than its anterior end, so that the angle between the sternal axis and the vertebral column approaches a right angle.

#### *Stage G* (Plate 16, figs. 218 and 219)

The two halves of the sternum have now concresced in the middle line from about the level of the first sternal rib to that of the fourth. The posterior lateral processes (*post lat pr*) have nearly attained their full length, but there is no trace of the posterior median process.

A transverse section (fig. 219) shows the corpus sterni to be slightly concave ventrad and somewhat thickened in the middle line, but devoid of any trace of a keel.

*Stages H and I* (Plate 15, fig. 204, and Plate 16, figs 220 and 221).

The two halves of the sternum are united, and the adult form is attained by the development of a well-marked posterior median process. There is the normal number (four) of sternal ribs articulated to the costal border, except in the specimen of *A. oweni* belonging to Stage H (fig 221), in which the fourth rib of the right side (*Th Rb 4*) does not reach the sternum. On the other hand, in one specimen of Stage I (fig. 204) the end of the fifth thoracic rib approaches within half a millimetre of the sternum (*cf* p 86).

*Stage K* (Plate 16, fig 222)

In one of the specimens belonging to this stage—a ripe embryo of *A. bulleri*—the sternum is still unossified, but in both the others—a ripe embryo and a newly-hatched chick of *A. australis*—the osteites of the costal sternum (pleurostea) have appeared (*Pl.ost*). In one of these specimens the posterior median process is double, in the other it is perforated by an oval foramen (fig 222, *fo*). This would seem to indicate a paired origin of the metasternum.

In neither of the specimens of *A. australis* are the adult proportions attained, the length of the corpus sterni being slightly less than half its breadth, as in *A. bulleri*. As will be seen by a comparison of figs. 222 and 208, of 220 and 212, and of 221 and 214, the proportional length increases considerably between late embryonic and adult life.

*Stage L* (Plate 16, fig 223)

The single specimen belonging to this stage has the pleurostea (*Pl.ost*) increased in extent, and is remarkable for the presence of three thin places (indicated by shading) in the body, one median and two paired, and evidently indicating recent extensions of cartilage. It looks very much as if the increase in proportional length were due to a filling up of the posterior notches. The posterior median process is perforated by a small foramen (*fo.*). The adult proportions are attained, the length of the corpus sterni being now considerably more than half its width.

*Stage M* (Plate 16, fig 224).

The pleurostea (*Pl.ost.*) have nearly met in the middle line, and have extended into the anterior lateral processes (*ant.lat pr.*), so that only the three posterior processes are unossified. The anterior border shows no trace of the sinuous curve found in the adult of this species (*A. oweni*).

In all later stages ossification is complete

## 4 THE SHOULDER-GIRDLE

*a. In the Adult.*

(Plate 16, figs. 225–232 )

The shoulder-girdle, like the sternum, is subject to great individual variation, and for purposes of comparison I have found it necessary to sketch it from the same points of view in all the adult specimens figured. In the front views (A in figs 225–232) the bone was placed with the distal end of the scapula and the whole sternal (epicoracoid) border of the coracoid resting on the table, and its outline traced on a sheet of glass placed immediately above it and parallel to the table. In the lateral or external views (B in the same figures) it was placed so that the glenoid fossa exactly faced the observer. The outline was taken on glass as before. In this way the relative dimensions of the various parts are shown from a fixed point of view. Both scapula and coracoid are considerably foreshortened in the front views owing to the curvature of the entire bone, but their correct length is given in the side views.

As a general rule, the scapula (*Scap*) is about one and a-half times the length of the coracoid (*Cor*), but in one specimen of *A. australis* (fig 227), it is hardly more than one and a-quarter times as long, and in a specimen of *A. owenii* (fig 231), it is more than twice as long. The curve of the scapula also varies considerably.

But it is in the coracoid that the most interesting variations occur. As a rule (figs. 230–232, A), it is a flattened bone with a nearly straight mesial and concave lateral border, but the mesial border is often (figs 227 and 228, A) somewhat excavated, and in three instances (figs. 225, 226, and 229, A) the excavation takes the form of a regular semicircular notch which is converted into a foramen (*cor fen*) by a ligament (*pr.cor lig*). The mere observation of the parts in the adult is enough to show what is clearly proved by their development (*infra*, pp 91 and 92), that the ligament is the degraded procoracoid, and that the foramen or notch is the coracoid fenestra which is so characteristic a feature in the shoulder-girdle of the Ostrich. In cases where there is no such fenestra, the bone in the corresponding position is always thin and transparent (indicated by shading in figs 227, 230, 231, and 232, A), the space being evidently filled up by the extension mesiad of the coracoid with the fibrous tissue stretched across it.

The small aperture, marked *Sup.cor for.* (fig 227, &c, A), and considered by both OWEN (24, p. 34), and my Father (43, Plate 17, fig 1), as the coracoid fenestra, is evidently homologous with the supra-coracoid foramen at the base of the procoracoid process in many Birds, and particularly well-marked in *Diomedea*, *Ocydromus*, &c.

In the Carinatae, the furcula is attached by ligament to three processes of the shoulder-girdle—the acromion (mesoscapula, W. K. PARKER) on the inner or preaxial border of the proximal end of the scapula, the procoracoid process (mesocoracoid process, W. K. PARKER) on the mesial or preaxial border of the coracoid at its dorsal

end, and the acrocoracoid of FURBRINGER (clavicular process, HUXLEY; head of the coracoid, proximal precoracoid, W K. PARKER) a large process from the anterior surface of the dorsal end of the coracoid towards its post-axial border. Thus, the foramen triosseum is bounded mesiad by the furcula, laterad by the acrocoracoid, and caudad by the acromion and procoracoid process, and the acrocoracoid is situated immediately mesiad of the tendon of the subclavius as it passes through the foramen triosseum to reach the dorsal aspect of the humerus.

In *Apteryx*, a fair proportion of the specimens examined have more or less well-marked tuberosities in the precise position of all the three processes referred to. At the ventral end of the scapula, close to its preaxial border, and immediately above the position of the obliterated coraco-scapular synchondrosis is an acromial tuberosity (*acr*) very obvious in figs 226, 228, and 230, at the dorsal end of the coracoid close to its preaxial border a less obvious, but undoubted procoracoid tuberosity (*pr.cor.t*) is shown in fig 230, and in every specimen the acrocoracoid tuberosity or spina coracoidea (*acr cor*) is a prominent feature. Moreover, the tendon of the subclavius (Plate 19, fig 293, *subcl.*) passes immediately mesiad of the last-named elevation, precisely as in *Carinatae*.

The coraco-scapular angle varies from  $150^{\circ}$  to  $122^{\circ}$ . It is largest ( $150^{\circ}$ ) in the skeleton in the Wellington Museum marked *A. maxima* (probably *A. bulleri*, fig 225), it is  $142^{\circ}$  in one specimen of *A. australis* (fig. 227) and in the supposed *A. haastii* (fig. 226), between  $127^{\circ}$  and  $130^{\circ}$  in another specimen of *A. australis* (fig 228), in one of *A. bulleri* (fig 229), and in one of *A. owenii* (fig 231); and  $122^{\circ}$  in two specimens of *A. bulleri* (fig. 230) and one of *A. owenii* (fig. 232). There is, therefore, no constancy in this respect in the various species. The fact that the angle is as small as  $122^{\circ}$  in *Apteryx*, while it rises to  $97^{\circ}$  in *Notornis* and to  $100^{\circ}$  in *Ocydromus* and *Diomedea* (26, p. 250) quite bears out FURBRINGER's statement that as a character distinguishing the *Ratitae* from the *Carinatae*, it is of considerably less importance than the relative size in the two groups of the acrocoracoid. FURBRINGER gives the range of variation in the coraco-scapular angle as  $130^{\circ}$  to  $160^{\circ}$  for *Ratitae*, and  $45^{\circ}$  to  $106^{\circ}$  for *Carinatae*, giving a difference of  $24^{\circ}$  between the two groups, the foregoing observations reduce the difference to  $16^{\circ}$ .

### *b Development of the Shoulder-Girdle*

*Stage E* (Plate 16, fig 216, and Plate 17, fig 233).

The absence of any stage of the shoulder-girdle earlier than this is much to be regretted, as I have been unable to ascertain whether there are originally formed separate chondrites for the coracoid, procoracoid, and scapula, as described by Miss LINDSAY (19). In the present stage the scapulo-coracoid consists of a solid bar of cartilage of much the same shape as the adult bone, but without any fenestrae or other signs to indicate the separation of coracoid and procoracoid. In fig. 233, taken

from the cartilage after removal from the body, the scapula appears to be nearly in the same straight line as the coracoid, but in fig 216, accurately reconstructed from sagittal sections, it is seen to be strongly curved, so that while the coraco-scapular angle, as usually taken, *i.e.*, considering the ventral end of the scapula only, is about  $135^{\circ}$ , it is only about  $83^{\circ}$  if the general direction of the scapula is taken by a line joining its base and apex. Fig 216 certainly suggests the straightening of the shoulder-girdle by its release from the backward pull of the shoulder muscles.

Another striking fact is that the long axis of the coracoid (fig 216, *Cor*) is inclined from its sternal articulation forwards, so as to make an acute angle with the vertebral column, instead of a right angle as in later stages (*cf.* fig 204, *Cor.*) In other words, the *coraco-vertebral angle* is about  $35^{\circ}$ , instead of  $90^{\circ}$ , and thus furnishes an important point of agreement with the *Carinatae*.

#### *Stages F and G* (Plate 17, figs. 234–236).

In these stages the shoulder-girdle has undergone very little advance except in size and in the increased development of the acrocoracoid tuberosity (*acr cor*), which is now a well-marked process considerably larger proportionally than in the adult. Its dimensions are well seen in fig 236, which shows two obliquely transverse sections through the junction of the scapula and coracoid in Stage G. Both pass through the acrocoracoid (*acr cor*), and B, which is three sections caudad of A, also passes through the supracoracoid foramen (*sup cor for*).

The coraco-vertebral angle is still acute, as shown by the fact that obliquely transverse sections of it were obtained by cutting an embryo (*A. australis*, Stage G) at right angles to the long axis of the trunk, but the inclination is considerably less than in the preceding stage, amounting to about  $60^{\circ}$  in Stage F.

#### *Stage H* (Plate 17, figs 237 and 238)

The two specimens belonging to this stage show a very important step in the development of the shoulder-girdle. In the younger of the two (*A. owenii*, fig 237) the scapula (*scap*) is ossified, but the coracoid has undergone no alteration, being still a solid cartilage with a very prominent acrocoracoid tuberosity.

In the other embryo (*A. bulleri*, fig 238) the scapula is similarly ossified, but the coracoid has undergone a great change, a portion of the cartilage having been absorbed so as to produce a large coracoid fenestra (*cor fen*) separating a narrow preaxial (mesial) procoracoid bar (*Pr Cor*) from a broad postaxial (lateral) portion, the coracoid proper (*Cor*), in which an ossification has appeared.

In *Apteryx*, therefore, the coracoid and procoracoid clearly result from a process of fenestration in an originally single cartilage. Whether this fenestration is a secondary process and the two elements arise in the first instance as distinct chondrites, my material has not allowed me to determine; but Miss LINDSAY'S researches (19, p. 692) show that such a mode of origin is probable. The



resemblance of the shoulder-girdle shown in fig. 238 to that of the Ostrich is very striking.

*Stages I and K* (Plate 17, figs. 239 and 240)

These stages are also interesting since they show the gradual degradation of the cartilaginous procoracoid.

In Stage I (fig. 239) the procoracoid (*Pr. Cor*) is a narrow cartilaginous bar continuous above with the coracoid, but free below, and connected by ligament with the epicoracoid region. In Stage K (fig. 240) the process has gone still further, and the procoracoid is almost entirely converted into ligament (*pr. cor. lig.*), only a small pointed process being left to indicate its dorsal end.

Stage L precisely resembles K, and in M the adult characters are assumed.

## 5. THE FORE-LIMB.

### *α. In the Adult.*

(Plate 17, figs. 241–253.)

With regard to the humerus, radius, and ulna, I have nothing to add to OWEN'S description, but his account of the manus is imperfect and somewhat obscure. He says "there is a minute carpal bone, two metacarpals, and a single phalanx," but the plate shows the manus to consist of three bones in a single longitudinal series. The middle and distal of these would naturally be considered as phalanges, so that there is only the proximal one to represent the carpal and the two metacarpals. The figure is on such a small scale that it is impossible to place much reliance upon it, but it has all the appearance of representing a normal wing of *A. australis*, while the description, at least as regards the separate carpal, applies rather to *A. oweni* (*vide infra*).

My Father (41, Plate 65, fig. 5) figures a manus which he calls *A. oweni*, but which is, in all probability, *A. australis*. In an earlier paper (42, p. 127) he figures a specimen in which a small radial carpal is shown, but is not referred to; the species in this case is not mentioned.

As far as my own observations go, the essential structure of the manus is quite constant in *A. australis* and in *A. oweni*, judging from four adult specimens of each; while in *A. bulleri* the variations are so great that the examination of five specimens is quite insufficient to determine their range. Besides these, I have examined the wing of one of the type specimens of *A. haastii* in the Canterbury Museum, as well as that of the supposed *A. haastii* from Puysegur Point (p. 38), and of the skeleton called *A. maxima* (= *A. bulleri*?) in the Wellington Museum.

In *A. australis* (fig. 241) the bones of the forearm (*Ra.*, *Ul.*) are succeeded by a somewhat irregular flattened bone, the carpo-metacarpus (*Cp. Mtcp.*). It presents on the preaxial side of its proximal border a small facet for the radius, and a larger

and very oblique surface for the ulna. Distad it narrows considerably, and gives attachment to the proximal phalanx. Postaxiad, it is usually produced into a tolerably well-marked projection, which represents the third metacarpal, a similar, but smaller projection, sometimes springing from the preaxial border, may represent the first metacarpal, but is possibly a mere process of the second. The development of this bone shows that it is composed of both proximal and distal carpals, and of the second and third, and possibly also the first, metacarpals.

There are sometimes two and sometimes three phalanges to the single (second) digit (*Phal* 2', *Phal* 2'', *Phal* 2'''), in the latter case the second or middle phalanx (*Phal* 2'') is always small, and, as will be seen, it appears later than the others. It is evidently obsolescent.

The presence of three phalanges to the index is a generalised character, the normal number in birds being two, but as, according to WIEDERSHEIM (52, p 218), three families of Carinatae possess the maximum number, no great stress need be laid upon the occasional presence of the second in *Apteryx*, except as showing which of the three has usually atrophied.

In *A. owenii* there seems to be invariably a distinct radiale (figs 242–244, *ra*) in the form of a small rounded nodule of bone intercalated between the radius and the carpo-metacarpus. In two of the specimens examined, the third metacarpal (fig 242, *Mtcp*. 3) is ankylosed along its whole length to the second (*Mtcp* 2) as in *A. australis*, but in the third it is free distad (fig 243), and in the fourth—a sub-adult specimen—united only by membrane (fig 244). The phalanges of the second digit may be three or two.

In *A. haastii* the single wing examined (fig 250) has two free carpals, a radiale (*ra*) and an ulnare (*ul.*), and all three phalanges are present.

In the skeleton, doubtfully referred to *A. haastii*, a radiale is present in the left manus (fig 251) but absent in the right (fig 252); there are also three phalanges on the left, and two on the right side.

In *A. bulleri* the variations in the structure of the carpo-metacarpal region are very striking. In two instances (fig 246) there is a single carpo-metacarpus exactly resembling that of *A. australis*. In a third (fig 245) the resemblance is equally close to *A. owenii*, there being a carpo-metacarpus and a radiale. In the fourth (fig 247) the radius and ulna on the left side articulate with a transversely elongated bone (*ra dist*) which apparently represents both the radiale and the distal carpals, and to the distal surface of which free second and third metacarpals are attached. It is worth noticing that this is probably the only recorded example of a fully adult recent bird with free metacarpals. On the right side of the same skeleton (fig. 248) the second metacarpal appears to have ankylosed with the carpals, forming an irregular rod-shaped carpo-metacarpus, while the third metacarpal is free. In the fifth and last specimen—removed like several others from a skin—there is (fig 249) a nodular radiale, a sigmoid bone which apparently represents the distal carpals and the second



metacarpal, and a short free third metacarpal. As far as I can make out there is no doubt about the species in any of the five cases

The Wellington specimen, marked *A. maxima*, agrees with the left side of the fourth example of *A. bulleri* mentioned above (fig 247). There is a single transversely elongated carpal (fig. 253), not yet ossified postaxiad, a large second metacarpal, or possibly carpo-metacarpal, and a small third metacarpal. Thus the characters both of the sternum and of the manus seem to show that this specimen is referable to *A. bulleri*.

It is worth mentioning that while the manus is usually permanently flexed postaxiad on the forearm at an angle of about  $140^\circ$  (figs 241, 245, &c), the two are sometimes nearly or quite in the same straight line (figs 243 and 250)

### *b. Development of the Fore-Limb.*

#### *Stage E.* (Plate 17, figs 254 and 255)

The external characters of the limb at this stage have been described (p 32). The humerus (*Hu*), radius (*Ra*), and ulna (*Ul.*) are well chondrified. The carpus is represented by a thickened plate of mesoblast, which in its external (dorsal) region (fig 255) shows no division into separate carpals, but towards the middle of its thickness (fig 254) presents four fairly well-marked patches of prochondral tissue, the rudiments of the carpals. Of these, one (*ra.*) is immediately distad of the radius, and is evidently the radiale, the other three lie proximad of the three metacarpals, and may be considered as the first (*dist. 1*), second (*dist. 2*), and third (*dist. 3*) distalia.

The three preaxial digits are quite distinct. The pollex consists only of a chondrified metacarpal (*Mtcp. 1*), the index of a metacarpal (*Mtcp. 2*) and proximal phalanx (*Phal. 2'*) of cartilage, and of a distal phalanx (*Phal. 2'''*) of prochondral tissue, the third of a chondrified metacarpal (*Mtcp. 3*) and a single phalanx of prochondral tissue.

#### *Stage F* (Plate 17, fig. 256).

There is still no trace of chondrification in the carpal mesoblast, and only two patches of prochondral tissue are distinguishable, one (*ra.*) between the radius and the first metacarpal, the other (*dist. 2*) immediately proximad of the second metacarpal. I take the first of these to be the radiale, the other the second distale.

The first (*Mtcp. 1*) and third (*Mtcp. 3*) metacarpals have not increased in size since the previous stage, but the second (*Mtcp. 2*) is half as long again. The distal phalanx of the second digit is still unchondrified, and there is no trace of a second phalanx, present in the embryo Goose, according to BAUR, in the third digit.

#### *Stage G* (Plate 17, figs. 257-260).

The carpals have begun to chondrify, but are still very indistinct, the several

chondrites fading insensibly into the common carpal mesoblast. In the specimen of *A. australis* belonging to this stage, a section taken near the dorsal (outer) aspect of the carpus (fig. 258) shows a distinct radiale (*ra.*) interposed between the end of the radius (*Ra*) and a large distale (*dist*). Further ventrad (fig. 259) the radiale is no longer seen, the radius is almost in contact with the distale, and a small chondrite (*ul*), probably an ulnare, is seen postaxiad of the third metacarpal (*Mtcp* 3). Fig. 257 shows my interpretation of these sections.

The first metacarpal (figs. 257 and 259, *Mtcp* 1) is represented only by a small rounded patch of cells, and seems therefore to have undergone complete histological degeneration. The second digit has two chondrified phalanges, and its metacarpal (*Mtcp* 2) has partly united with the distale. The third consists only of a small metacarpal (*Mtcp* 3).

In the specimen of *A. owenii* belonging to this stage (fig. 260) the skeleton of the wing was dissected out and afterwards cut into serial sections in order to settle some doubtful points. It is quite possible that the carpus may have been injured in dissection. There is a large chondrite (*cp.*) imperfectly chondrified distad, and giving attachment on the one hand to the radius and ulna, and on the other to the first and second metacarpals. It apparently represents the first and second distalia, whether it includes also the radiale or whether the latter was lost in preparation is uncertain. Immediately postaxiad of it is an unchondrified but distinct patch of mesoblast (*dist* 3), with which the third metacarpal is connected. It is probably the third distale. Postaxiad of this again, and passing obliquely proximad towards the ulna is a rod-shaped chondrite (*ul*) which appears to be an ulnare.

The first metacarpal (*Mtcp* 1) is well developed in this specimen, and ossification has begun in the shafts of the humerus, radius (*Ra*), and ulna (*Ul*).

### *Stage H* (Plate 17, figs. 261 and 262)

The humerus, radius, and ulna have their shafts ossified, but the manus is still entirely cartilaginous, and its structure differs considerably in the two specimens belonging to the stage.

In *A. owenii* (fig. 261) there is a large radiale (*ra*), and the distalia have united into a single transversely-elongated cartilage (*dist*) which articulates proximad with the radiale and the ulna, and distad with the second and third metacarpals. It is obvious that by subsequent concrescence of this cartilage with the metacarpals the carpo-metacarpus of the adult is formed.

The third metacarpal (*Mtcp* 3) is about the same length as the second (*Mtcp* 2), and its distal end is turned slightly postaxiad. Both metacarpals are in process of fusion with the distale. There is no trace of a first metacarpal. The second digit bears two phalanges, of which the distal one is very small.

There are synovial capsules between the radius and radiale, the ulna and distale,

and the radiale and distale, as well as between the metacarpal and proximal phalanx of the second digit

In *A. bulleri* (fig. 262) there is a large cartilaginous preaxial carpal (*ra.dist.*) articulating proximad with both radius and ulna, and distad with both second and third metacarpals. The ulna and the second metacarpal project postaxiad of it, and between them is intercalated a small nodular cartilage (*ul.*). Comparison with other stages leads me to consider the large preaxial carpal (*ra.dist.*) as a radio-distale, the small nodule (*ul.*) as an ulnare.

The third metacarpal is—quite exceptionally—longer than the second and of equal diameter. The second digit bears two phalanges, the distal of which has taken on the usual characters of an ungual phalanx.

### *Stage I* (Plate 17, figs. 263 and 264)

The two specimens, like those of the previous stage, show very considerable differences.

In *A. australis* (fig. 264) there is a large radiale (*ra.*) and a small trigonal ulnare (*ul.*). Articulating with these, and partly also with the ulna, is a large flat distale (*dist. 2*), the postaxial end of which (*dist. 3*) is shown by sections to be a separate chondrite, its plane of junction with the larger cartilage being marked by a layer of small close-set cells. The second metacarpal is in contact mainly with the larger cartilage, the third with the smaller, they may, therefore, be safely considered as the second and third distalia.

The second and third metacarpals have undergone almost complete concrescence with the distalia, the junction between them being marked only by a layer of close-set cells. The second metacarpal (*Mtcp. 2*) is slightly longer and considerably wider than the third, and its shaft is ossified; the third (*Mtcp. 3*) is slender, pointed distad, and separated by a space from the second, except at its proximal end where concrescence has begun.

The second digit bears three phalanges, of which the first (*Phal. 2'*) has begun to ossify in the middle of its shaft, and the third (*Phal. 2'''*) at its distal end; the second (*Phal. 2''*) is considerably smaller than the others, and is unossified.

As in the previous stage, there is a distinct synovial capsule between the radiale and the distale, as well as between the radius and ulna respectively, and the carpus.

The specimen of *A. bulleri* belonging to this stage (fig. 263) presents certain peculiarities. The carpus consists of a distinct radiale (*ra.*) and of a large distale (*dist.*) nearly fused with the second metacarpal. The third metacarpal is free, and slightly smaller than the second.

The preaxial border of the second metacarpal is produced into a blunt process (*Mtcp. 1*), which is shown by sections to be a distinct chondrite; it can hardly be anything else than the first metacarpal which has thus, in this instance, fused with the second, instead of degenerating.

There are only two phalanges to the second digit, the second being absent. The third (*Phal.* 2''') has its tip ossified, and gives off from its proximal end a rod-like recurrent process (*Phal* 3), which appears to be a distinct chondrite, it is probably the distal phalanx of the third digit, which has not, as usual, atrophied at an early stage

*Stage K* (Plate 18, figs. 265–268)

In this case also there is a striking difference between the two specimens examined

In *A. australis* (figs 265 and 266) the carpo-metacarpus is almost exactly intermediate between the condition found in the previous stage and in the adult. The radiale (fig 266, *ra*) and ulnare (*ul*) have begun to coneresce with the distalia (*dist*), the synovial space existing between them in Stages H and I being nearly filled up by small cells, which shade into the cartilage on either side. Towards the ventral (palmar) aspect of the carpus the radiale and ulnare have united. The distalia (*dist*) have completely fused with the metacarpals. The diaphysis of the second metacarpal has extended so that the shaft of the bone is now well ossified, and the third metacarpal (*Mtcp* 3) has united with it, forming a narrow cartilaginous ridge postaxiad of the bone.

In the left manus there is a small cartilaginous projection (fig 265, *Mtcp* 1) on the preaxial side of the carpo-metacarpus, probably representing the first metacarpal.

In *A. bulleri* (figs 267 and 268) the condition of the parts approaches most nearly to what was found in the same species in Stage H (fig. 262). There is a large radio distale (*ra.dist*) separated by a very thin layer of fibrous tissue from the second metacarpal, with which it is beginning to unite. There is no ulnare, but its place is occupied by a well-defined patch of fibrous tissue. The second and third metacarpals are separate, and each has a distinct diaphysial ossification.

*Stage L* (Plate 18, figs. 269–271)

In a specimen of *A. australis* a few weeks old the radiale and ulnare (fig. 270, *ra.*, *ul.*) have united with one another, and their concrescence with the distalia (*dist*) is nearly complete. The ossification of the second metacarpal has extended both into the distalia and into the third metacarpal. Hence from an external inspection (fig. 269) the manus presents the simple carpo-metacarpus characteristic of the species.

In the wing of a young *A. oweni* removed from a skin, and apparently referable to this stage (fig. 271), there is a cartilaginous radiale (*ra*), and the first and third metacarpals are represented by distinct osteites. The first (*Mtcp* 1) is a rounded nodule lying preaxiad of the proximal end of the second metacarpal (*Mtpc* 2); the

third (*Mtcp.* 3) is a rod of bone tipped with cartilage lying close alongside its post axial border.

*Stage M* (Plate 18, figs 272 and 273).

The specimen of *A. oweni* belonging to this stage (fig 273) is the only instance I have met with of any important deviation from the normal type of the species. Distad of the radius there is, instead of the ordinary nodular radiale, a semilunar bone (*ra*), which extends distad a short distance along the preaxial border of the carpo-metacarpus, and seems to consist of radiale *plus* first metacarpal. The third metacarpal (*Mtcp* 3) is free, and is tipped with cartilage.

In a wing removed from a young stuffed specimen of *A. australis*, which may be referred to this stage (fig. 272), there is a distinct osteite (*ul.*) at the postaxial extremity of the cartilaginous proximal end of the carpo-metacarpus. It is obviously an ulnare

## 6. THE PELVIC GIRDLE

### *a. In the Adult.*

I have nothing to add to the descriptions of OWEN (24) and of MITVART (21) except to mention that the curvature of the ischium appears to be slightly but constantly greater in *A. oweni* and *A. bulleri* than in *A. australis*, and to call attention to a statement of OWEN's which seems to imply the presence of a perfectly new and unique element in the vertebrate skeleton. He says, "A distinct epiphysial piece of bone, of a compressed and triangular form, is wedged in between the posterior extremity of the ilia and the first three caudal vertebræ."

The bone in question is nothing but the ankylosed neural spines of the first three caudal vertebræ. In one of my specimens it is separated by a well-defined groove from the corresponding centra, and shows no distinction into its constituent parts, it is, however, united both with the centra below and with the ilia above.

### *b. Development of the Pelvis.*

*Stage D* (Plate 18, fig. 274, and Plate 15, fig. 193).

The pelvic girdle, in this stage, corresponds pretty nearly with Miss JOHNSON's fig 7 (18, Plate 27). The pre-ilium (*Pr.Ilm.*) is short, the post-ilium (*Pt.Ilm.*) longer and strongly curved ventrad, the pubis (*Pub.*) slender and nearly straight, the ischium (*Isch.*) broad and expanded distad. The pectineal process (*pect.pr.*) is slightly below the level of the acetabulum, springing obviously from the pubis and not from the ilium, and both pubis and ischium are nearly at right angles to the long axis of the body, as shown by the fact that a vertical section through the acetabulum takes in nearly the whole length of the ischium (Plate 15, fig. 193).

The ischium and pubis are not continuous, as in Miss JOHNSON's figures, but are separated by a layer of indifferent tissue extending downwards from the acetabulum.

*Stage E* (Plate 18, fig 275)

The more advanced condition of the pre- than of the post-ilium is very obvious. The post-ilium (*Pt Ilm*) has attained its adult proportions, *i e.*, is of about the same length as the ischium and pubis, it is also curved downwards, as in the adult, and has altogether a finished appearance. The pre-ilium (*Pr Ilm*), on the other hand, is very thin, ends in an irregular border, and falls far short of its ultimate dimensions. These facts certainly lend support to the view that it is the post-ilium of Birds which answers to the ilium of Reptiles, and that the pre-ilium is a secondary structure.

The distinctness of the pubis and ischium is well seen both in a dissection and in sections, there is a well-defined tract of fibrous tissue passing vertically downwards from the acetabulum, and separating their proximal ends from one another.

*Stage F* (Plate 18, fig 276)

The most marked change is the forward extension of the pre-ilium (*Pr Ilm*), which has attained its ultimate length, although its dorsal region is still imperfect. The pubis and ischium are now distinctly inclined backwards.

*Stage G* (Plate 18, fig 277).

The adult form is assumed, the pre-ilium being perfectly formed, and the pubis and ischium having rotated backwards to their final position. There is no appearance of ossification.

*Stages H-L* (Plate 15, fig 204, and Plate 18, fig. 278)

The three divisions of the pelvis are now separately ossified. In H, the anterior and posterior borders of the ilium are still cartilaginous, and the pubic osteite is a rod-shaped bone, not more than half the length of the cartilage, and situated at its proximal end. In I and K (fig. 204) ossification has extended farther, and in L (fig. 278) the only cartilaginous parts are the distal ends of the pubis and ischium, the antitrochanter (*Ant.Trch.*), and the pectineal process (*pect pr.*), together with a narrow tract between the pubis and pre-ilium.

*Stages M-O* (Plate 18, fig 279).

In Stage M, the ossifications have extended into and obliterated the connecting cartilages, but have not yet ankylosed. In Stage N (fig 279) the pectineal process (*pect pr*) is seen to be ossified equally by the ilium and pubis. This is also the case in the Ostrich, according to HATCHETT JACKSON (48, p. 65).

In Stage O, complete ankylosis has taken place.



## 7 THE HIND-LIMB.

*a. In the Adult*

(Plate 18, fig 292 )

The hind-limb of *Apteryx* is so typically avian, and has been so thoroughly described by OWEN, that little need be said about it here. It is necessary, however, to supplement his account in one particular.

OWEN states (24, p 37) that "there is a small cuneiform tarsal wedged into the outer and back part of the ankle-joint." In his 'Anatomy of Vertebrata' (vol 2, p 83), the same bone is called a "calcaneal sesamoid," and is said to exist also in several *Rasores*\*. It occurs as an ossification in the thickness of the postaxial moiety of the mesotarsal articular pad (fig 292, *cent* 2) and has therefore all the appearance of a sesamoid bone. Its development shows, however, that it is formed by the ossification of a distinct chondrite which has the relations of a postaxial centrale. At the time my Preliminary Note (28) was written I was not aware that it had been figured by MORSE, and figured and described by my Father. It is about 5 mm long in the adult *A. owen* and 7 mm long in the larger species.

I also find in the supposed skeleton of *A. haastii* and in the right leg of one skeleton of *A. australis* a similar but much smaller bone (fig. 292, *cent.* 1), about 4 mm in diameter, imbedded in the lesser or preaxial moiety of the mesotarsal pad. This is also formed by ossification of a distinct chondrite, which however does not appear, as far as my observations go, until after hatching. It may be looked upon as the first or preaxial centrale. I have not found it in *A. owen*.

*b. Development of the Hind-Limb*

*Stage D* (Plate 18, figs. 280-282).

The femur (*Fe.*) is very slightly shorter than the crus, and the tibia (*Tib.*) and

\* The bone in question occurs also in *Dinornis*, and thus furnishes an additional point of resemblance between that genus and *Apteryx*. It is apparently not mentioned by OWEN in his memoirs on the Moa, but was described and figured, in 1874, by COUGHTREY (8a), in the remarkably perfect, and, indeed, unique feet of *D. ingens*, now in the Otago University Museum. It is also present on both sides in a very fine "individual" skeleton of *D. robustus*, in the same collection. COUGHTREY describes the ligamentous attachments of the bone, which, following OWEN, he calls a "calcaneo-sesamoid." BULLER (8, vol. 1, p 32, and vol 2, p 334), describes and figures it as an "astragalus-like bone," in a foot of *D. elephantopus*, in the Cambridge Museum, and mentions its occurrence in the well-known skeleton of *D. robustus*, in the York Museum; he refers to COUGHTREY's paper, but has overlooked the fact that the bone is described there, stating that it has not hitherto been noticed in *Dinornis*.

There is another point in the structure of the foot of *Dinornis* which is often wrongly stated in authoritative publications. VON HAAST erroneously concluded that the Dinornithidæ as restricted by him, differed from the Palapterygidæ in the absence of a hallux, but as HUTTON showed in 1876 (15), and as is abundantly proved by the collections in the Otago University Museum, this is not the case, many individual feet of Dinornithidæ having been found with a well-developed hallux.

fibula (*Fib*) are equal in length and sub-equal in diameter. The tarsus consists of the three chondrites usual in embryo Birds, a large tibiale (*tib*), a small fibulare (*fib*), and a large, single, transversely-elongated distale (*dist*).

All five digits are present. The hallux (fig 281, *Mt tsl* 1) is a rounded nodule of cartilage close alongside the proximal end of the second metatarsal (*Mt tsl* 2) and separated by indifferent tissue from the distale. The second digit consists of a metatarsal and one phalanx, the third and fourth each of a metatarsal and two phalanges, and the fifth (fig 282, *Mt tsl* 5) of a short conical cartilage attached by its proximal end to the fibulare and by its preaxial border to the distale.

#### *Stage E* (Plate 18, figs. 283 and 284).

The fibula is still of the same length as the tibia, but not more than half its diameter. Its distal end is pointed. The tarsals are as in the preceding stage, except that the tibiale and fibulare are very closely applied to the end of the tibia.

The hallux has shifted distad, being attached to about the middle of the second metatarsal, it consists of a metatarsal (*Mt tsl* 1) and one phalanx. The fifth digit is still a distinct pointed cartilage (*Mt tsl* 5) but has begun to degenerate, being absolutely as well as relatively smaller than in the previous stage.

#### *Stage F* (Plate 18, figs 285–288)

The fibula is still further reduced in size and no longer reaches to the distal end of the tibia. The tibiale (figs 285 and 287, *tib*) has sent off the ascending process (*asc.pr*) which extends proximad along the anterior (external) face of the tibia, and neither in this nor any other stage shows the slightest indication of being a distinct chondrite comparable to an intermedium. The fibulare (fig. 286, *fib*) is still distinct but smaller proportionally than in previous stages. The mesotarsal joint has made its appearance (fig 287) by the intrusion of a mass of connective tissue—the rudiment of the articular pad—between the tibiale and the distale on the posterior (flexor) aspect of the limb. On the postaxial side a concentration of nuclei in this tissue (*cent* 2') indicates the position of the second or postaxial centrale.

It is worth mentioning that the articular pad does not appear to be a syndesmosis (*cf* 14) i.e. a fibrous pad formed, like the cartilages it separates, from the common blastema of the limb, but to be formed of connective tissue, unconnected with the limb-rudiment, which intrudes between the proximal and distal tarsals on the appearance of the mesotarsal flexure. Its origin appears therefore to support SUTTON's view (50) of the origin of interarticular cartilages, viz., that they are modified tendons which have become drawn in between the opposed surfaces of the bones forming the joint. This being the case the question naturally arises whether a nodule of hyaline cartilage appearing in such a structure can be properly counted as a tarsal. I think, however, that the fact of the two chondrites which I consider as centralia making



their appearance in this way may be accounted for on the hypothesis that, being vestigial or obsolescent structures, their origin is greatly retarded

The hallux (fig 285) has nearly reached its adult position, and the second, third, and fourth digits have acquired their full number of phalanges. The rudiment of the fifth digit (fig 288, *Mt ts1* 5) has undergone histological degeneration, being no longer formed of hyaline cartilage but of indifferent tissue. It is also greatly reduced in size, being only 0.25 mm long as against 0.6 mm in Stage E, and 1.2 mm in Stage D (cf figs 282, 284, and 288, which are all drawn to the same scale). It is, therefore, evident that the fifth digit undergoes gradual degeneration in *Apteryx* instead of concurring with the fourth metatarsal, as in the Chick (3)

#### *Stage G* (Plate 18, figs 289–291)

The adult form is assumed in all essential respects (fig 289). The shafts of the femur (*Fe*) and tibia (*Tib*) are ossified in about their middle thirds, and in one specimen (*A. australis*) bone has also appeared in the fibula.

The tibiale has partly fused with the tibia and the fibulare (fig. 290, *fib*) with the tibiale. The concrescence is, however, incomplete, some sections showing both cartilages as distinct structures. The distal surface of the tibiale has assumed its normal pulley-like form. The intrusive connective tissue from which the mesotarsal articular pad is formed has increased greatly in quantity (fig. 291), and the postaxial centrale (*cent.* 2) appears in it as a distinct rounded nodule of cartilage.

The distale (*dist*) has partially fused with the second and fourth metatarsals (figs 290 and 291), but the third (fig 291) is still free.

#### *Stage H.*

Ossification has greatly advanced, the thigh and shank bones having well ossified shafts. The tarsals are still cartilaginous, but the metatarsals are bony, with the exception of that of the hallux. They are still free and are readily separable both from one another and from the distale. In the second and third digits all the phalanges are ossified, but in the fourth, the 2nd–5th phalanges are cartilaginous. Perhaps the late appearance of ossification in this digit may be looked upon as the first step in the process which, in the Ostrich, has resulted in its complete atrophy.

#### *Stage I.*

Ossification has advanced further, all the phalanges as well as the first metatarsal being bony.

#### *Stages K and L.*

Endosteal deposits of bone have appeared in both tibiale and distale, and the second, third, and fourth metatarsals are firmly ankylosed. In K the mesotarsal pad encloses a single postaxial chondrite, but in L a second much smaller nodule or

cartilage is present in the preaxial moiety of the pad. This is the first or preaxial centrale.

### *Stage M*

This specimen differs from the adult only in having the tibiae still free from the tibia and the distale from the metatarsus, and in the centrale being still cartilaginous.

## VI—THE MUSCLES OF THE WING

(Plate 19, figs 293–296)

OWEN's description of the muscles of the wing is incomplete in certain particulars.

In the specimens examined by me there is no pectoralis tertius, but only a pectoralis major (fig 293, *pect maj*) and a pectoralis secundus or subclavius (*subcl.*), both of which correspond with OWEN's description. The account of the coraco-brachialis is hardly correct. The coraco-brachialis superior (*cor brach sup*) is a large muscle arising from the dorsal half of the postaxial border of the coracoid and inserted into the proximal third of the humerus. The coraco-brachialis inferior (*cor.brach.inf*) is a much smaller muscle arising from the ventral half of the postaxial border of the coracoid and inserted by a short tendon into the head of the humerus.

After describing the muscles of the shoulder OWEN concludes his account of the myology of the wing as follows —

“A minute flexor, wanting the attachment to the scapula which exists in birds of flight, and arising solely from the humerus glides along the front of that bone, chiefly as a delicate tendon to be attached to the inner part of the ulna.

“A single extensor, almost equally tendinous and delicate, arises from the scapula and represents the ‘long extensor’ of VICQ D’AZYR. It is inserted into the rudimental olecranon.

“There is a tendinous trace of a flexor and extensor of the minute monodactyle manus, but the motions of the rudimental wing and its terminal hook would seem to be produced as much by the cutaneous muscles which converge to be inserted into the integument connected with it, as by the feeble representatives of the true wing-muscles above described.”

This account is imperfect in many particulars. Both biceps and triceps are incorrectly described, and the muscles of the forearm are entirely overlooked. The omission to notice them is probably due to the very thick and tough fascia by which they are covered, although it must be remembered that the great variability of the entire wing may account for many discrepancies between the present account and that just quoted. It is a curious circumstance that whenever subsequent observers have had occasion to correct the original description of *Apteryx*, the result has been to show the bird to be less aberrant and more typically avian than it was considered

to be by the distinguished anatomist to whom we owe our first knowledge of its structure.

The *biceps* (fig 293) is a long slender muscle fleshy in about its middle third. It arises by a single tendon from the acro coracoid tuberosity (*acr.cor.*), and is inserted, also by an undivided tendon, into the radius at about the junction of its proximal and middle thirds.

The *triceps* is a slender, two-headed muscle. The long head arises from the post-axial border of the scapula immediately dorsad of the glenoid cavity and passes outside the teres to join the short head which arises from the distal three-fifths of the dorsal surface of the humerus. The triceps is inserted by a broad tendon into the olecranon.

The *brachialis anticus* (figs. 293, 294, and 296, *brach.ant.*) is a small muscle arising from the distal eighth of the ventral (flexor) surface of the humerus and inserted into about the proximal sixth of the radial surface of the ulna.

Lying immediately mesiad of the preceding is a small triangular muscle (fig 296, *brach.ant.access.*) with very similar origin and insertion. It arises from the internal tuberosity of the humerus and is inserted into the proximal end of the ulna. It may be called the *brachialis anticus accessorius*, and is probably due to a duplication of the small flexor of the forearm such as is occasionally found in Mammals. It was present in two wings of *A. bulleri*, but was absent on both sides of the specimen of *A. australis* on which most of my observations were made.

The *anconeus* (figs 293 and 295, *ancon.*) arises by a flat tendon from the external tuberosity of the humerus, its fibres diverge in a fan-like manner, and are inserted into the greater part of the outer surface of the shaft of the ulna. SELENKA (49) makes no mention of this muscle. MORRISON WATSON (51) failed to find it in Penguins, in some genera of which it is said by other observers to exist. It must act partly as a pronator.

The single *supinator* (figs. 293 and 295, *supin.*) arises with the preceding muscle from the external tuberosity of the humerus, and is inserted into the anterior (preaxial) border of the shaft of the radius.

The single *pronator* (figs. 294 and 296, *pron.*) arises by a flat tendon from the internal tuberosity of the humerus. its fibres diverge, and are inserted into the distal two-thirds of the inner (flexor) surface of the radius.

As the pronator on the inner may be said to balance the supinator on the outer surface of the forearm, so the externally situated anconeus is balanced by a very similar muscle (figs. 294 and 296, *flex.prot.int.*) which arises from the internal tuberosity of the humerus, and is inserted by diverging fibres into the inner (flexor) face of the distal two-thirds of the ulna. It appears to answer to the *flexor profundus interior gallinaceorum* of SELENKA (49), which is well developed in the common fowl, but has nothing like the same proximo-distal extent as in *Apteryx*. It also seems to

correspond with the muscle called *supinator accessorius* by MIVART (22) in *Iguana*. In the specimen of *A. australis* examined, the tendon of origin of this muscle crosses that of the pronator (fig 294)

The *extensor carpi ulnaris* (figs 293 and 295, *ext carp ul*) is a very slender muscle, arising in common with the supinator, of which, proximad, it forms a part. Its fleshy portion is extremely small, and soon passes into a long and very delicate tendon, which is inserted into the dorsal surface of the carpo-metacarpus, near its postaxial border. In a specimen of *A. bulleri* (fig 295) this muscle was entirely tendinous.

The *extensor indicis proprius* (figs 293 and 295, *ext ind prop.*) is a small muscle arising from the contiguous surfaces of the radius and ulna. Distally it passes into a strong tendon which, in the specimen of *A. australis* (fig 293), could not be traced beyond the middle of the carpo-metacarpus, but in that of *A. bulleri* (fig 295) is inserted into the base of the distal phalanx of the single (second) digit. I call this muscle an extensor indicis rather than an extensor digitorum communis because of its origin.

The *extensor metacarpi radialis brevis* (figs 293 and 295, *ext metacarp rad brev.*) is a very small muscle, arising with the preceding from the contiguous surfaces of the radius and ulna, and passing distad into a slender tendon, which curves preaxiad over the dorsal surface of the carpo-metacarpus to be inserted into its proximal border.

The *flexor digitorum profundus* (figs 294 and 296, *flex dig prof*) is a small muscle arising with the two preceding from the contiguous surfaces of the radius and ulna. It is continued into a rather broad flat tendon which passes along the inner (flexor) face of the carpo-metacarpus and proximal phalanx, and is inserted into the base of the distal phalanx.

In one specimen (*A. australis*) a minute tendon (fig 294, *flex carp. rad*) was seen preaxiad of that of the deep flexor, and passing to the preaxial side of the carpo-metacarpus. probably it is a vestigial *flexor carpi radialis*.

In one specimen of *A. bulleri* a few fleshy fibres (fig 295, *interos. dors*) were seen on the dorsal face of the carpo-metacarpus, and immediately preaxiad of the extensor indicis tendon. they probably represent an *interosseus dorsalis*.

The wing of *Apteryx* is thus seen to have the usual flexors and extensors of the forearm, and a rather unusually large development of muscles acting as pronators and supinators for so small and obviously vestigial an organ. There is also a fair-sized flexor and an equally large extensor of the single digit, as well as two small extensors and a minute flexor of the carpo-metacarpus.

The evidences of degeneration are very clear, and the variability of the muscles is noteworthy, the two specimens examined differing considerably in minor points.

The differences in the myology of the wing between the Kiwi and the Ostrich

(20, p. 549) are very marked. I have not been able to consult any detailed description of the wing-muscles in the other Ratitæ

## VII—THE BRAIN

### *a In the Adult.*

(Plate 19, figs 297–303)

The brain and cerebral nerves of *Apteryx* are described by OWEN in a supplementary memoir (24, *b*) illustrated by several figures. As, however, the description is imperfect in some particulars, and the figures small, and drawn from specimens from which the pia with its bloodvessels had not been removed, I have thought it advisable to preface the account of the development of the brain by a brief description of the adult organ taken from well-preserved brains of *A. australis* and *A. bulleri*. The terminology employed<sup>1</sup> was suggested in a short paper in 'Nature' (29).

Comparing the brain of *Apteryx* with that of other Birds, *e.g.*, the Turkey, figured by HUXLEY (16, pp. 302 and 303), the Goose, Gull, and Eagle by OWEN (25, pp. 118 and 119), and the Pigeon by WIEDERSHEIM (53, p. 165) and myself (27, pp. 255 and 259), one is struck with the proportionally large size of the cerebral hemispheres (fig 297, *Prosen.*), and with the way they overlap the cerebellum (*Epen.*). In this respect *Apteryx* resembles the Passerine Birds more closely than the comparatively generalized Gallinæ and Columbæ. As in other Birds, the outline of the cerebellum is roughly semicircular from before backwards (figs. 299 and 301), and is marked externally by grooves, which radiate from the flocculus (*floc.*): in Carinatae the grooves on the anterior, as well as those on the posterior moiety of the epencephal are visible externally, while in *Apteryx* the anterior ones are completely hidden, the hemispheres extending as far back as the flocculi. As a consequence of this, the pineal peduncle (fig 301, *Pin*), instead of being vertical, is inclined backwards.

Another peculiarity is the position of the diencephal, which is best seen in a sagittal section (fig. 301). In most Birds the lamina terminalis looks directly forwards, the optic chiasma downwards, while the foramen of MONRO is in the antero-dorsal angle of the diacœle, or third ventricle, and the anterior commissure just beneath it. In *Apteryx* the whole of this division of the brain is as it were tilted backwards. the lamina terminalis (*lam.term.*) looks upwards, and the optic chiasma (*opt.chs.*) forwards, the foramen of MONRO (*for.M.*) is in the postero-dorsal angle of the diacœle (*di.cœ*) and the anterior commissure (*ant.com.*) in the middle of its dorsal wall. In the same way, the optic commissure (*opt.com.*), or thin roof of the iter, is vertical, instead of horizontal.

The combined anterior commissure (*ant.com.*) and corpus callosum (*corp.call.*) is unusually large, the posterior commissure (*post.com.*) small. The pineal body (figs. 29 and 301, *Pin*) has the usual form; the pituitary body (*Pty.*) is globular and connected with a narrow conical infundibulum (*inf.*).

The relations of the more important cavities of the brain, including the small optocœles or ventricles of the optic lobes (*opt cœ*) are shown in figs 300–303.

The numerous olfactory nerves are given off from the ventral and anterior surfaces of the rhinencephal (*Rhnen*), and pass, some almost directly downwards, others forwards, to the Schneiderian membrane (See Plate 13, figs 157 and 158, *Nv I*)

The small optic nerves (*Nv II*) pass from the chiasma downwards and forwards to the eye. The nerves of the eye muscles (*Nv III*, *Nv. IV*, *Nv VI*) have the usual relations, their mode of exit from the skull has already been described (pp 46 and 47)

The trigeminal (*Nv V.*) is said by OWEN (24, p 324) to leave the cranium before dividing, but this not the case. Its root lies immediately over the trigeminal foramen (Plate 14, fig 167, *Nv V*), and it divides shortly after its origin into two trunks, one of which—the common trunk of the second and third divisions (fig 167, *Nv. V<sup>2,3</sup>*)—passes downwards and forwards through the trigeminal foramen, while the other—the first division or orbitonasal nerve (figs 164–166, *Nv. V<sup>1</sup>*)—passes forwards along the surface of the orbitosphenoid bone, finally making its exit from the skull by the orbitonasal foramen (figs 162 and 163, *Nv V<sup>1</sup>*). The sections of Stage H show conclusively that OWEN is in error when he says that it is the ventral ramus of the orbitonasal which supplies the tactile organ at the end of the beak, while the dorsal ramus “becomes lost upon the septal membrane”, as a matter of fact it is the dorsal ramus (figs. 149–157, *Nv V<sup>1a</sup>*) which supplies the tactile organ; the ventral ramus (*Nv V<sup>1b</sup>*) supplies the outer surface of the beak.

The seventh nerve (figs 298 and 299, *Nv VII.*) arises from the lateral region of the metencephal (*Meten*), behind and above the root of the fifth, it is immediately followed by the eighth (*Nv. VIII*) which, as already stated (p 45), divides into two main and about three smaller branches, which enter the auditory capsule through separate foramina. There is nothing of special interest in the origins of the ninth to the twelfth nerves (*Nv IX*, *X*, *XI.* and *XII*)

#### *b. Development of the Brain.*

My observations on this subject are very imperfect owing to lack of material; they are however not without interest, since they seem to prove conclusively what might have been inferred from adult anatomy that the brain of *Apteryx* is simply a typical avian encephal with reduced optic lobes

*Stages A and B* (Plate 4, figs. 17, 18, and 22–30)

The metencephal (*Meten.*) has already undergone a considerable thickening of its floor, while its roof is very thin, the cerebellum or epencephal (fig. 17, *Epen*) is indicated merely by a thickening of the antero-dorsal region of the hind-brain. The floor of the metacœle or fourth ventricle (*mt cœ.*) has an undulating antero-posterior



contour (fig. 17), the depressions probably correspond with the doubtful encephalomerites into which this region of the brain is frequently divided.

The mesencephal, as already seen from an external view (Plate 3, figs 1 and 2, *Mesen.*), is small, and shows no indication of optic lobes on its dorsal surface.

The diencephal is large, and contains a spacious diacœle or third ventricle (*di cœ*). The pineal body (figs. 17 and 18, *Pin*) has the form of a narrow diverticulum, and immediately cephalad of it is a second out-pushing of the roof of the diacœle (*Pr Pin Divert*) which I have not seen mentioned. It is very different in form from the pineal offshoot, being expanded at its origin, and narrowing almost to a point distad. This structure, which apparently gives rise to the velum interpositum, may be called the *prepineal diverticulum*.

The ventral region of the diencephal is dilated to form the infundibulum (*inf*) to which the pituitary out-pushing of the stomodæum (*Pty.*) is closely applied. Its lateral regions give off the optic vesicles (fig. 24, *Opt ves.*) which are already invaginated.

The prosthiencephal (secondary fore-brain, unpaired cerebral rudiment) has already divided into a median portion, the basi-cerebrum, containing a wide cavity, the aula (figs. 17, 22, and 23), and paired offshoots, the prosencephals or cerebral hemispheres, containing large prosocœles or lateral ventricles (fig. 22, *prs.cœ.*), the walls of which are still of approximately equal thickness throughout.

#### *Stage C* (Plate 5, figs 34-42).

The metencephal and epencephal (fig. 36, *Epen.*) have undergone comparatively little alteration, but in the other divisions of the brain changes of considerable importance have taken place.

The mesencephal, although still simple in front (fig 34, *Ms.cœ.*), has divided posteriorly into a median ventral portion, the basi-opticus (fig. 35, *Bs.Opt.*), and paired offshoots, the optic lobes (*Opten*). Corresponding with this the mesocœle, which is still a simple cavity in the anterior part of the region (fig. 34, *Ms.cœ.*), is distinguishable into a median iter (fig 35) and paired optocœles (*Opt.cœ.*).

In the fore-brain the posterior or outer walls of the prosocœles (fig. 34, *Prs.cœ.*) have undergone a considerable thickening, forming the rudiments of the corpora striata (*corp stri*). The aula is reduced to a small cleft, communicating by narrow apertures, the foramina of MONRO (*for M*), with the prosocœles.

#### *Stages D-F* (Plate 19, figs. 304-307).

The brain has advanced immensely between Stages C and D, but very little change is noticeable between D and F, the chief differences being the greater size and rounder form of the hemispheres in the later stage (*cf* figs. 304 and 306).

As shown by a sagittal section (fig. 307), the flexure between the fore- and hind-brain is at its maximum. The metencephal (*Meten.*) has practically assumed its adult



characters, except for its strong sigmoid flexure, but the cerebellum (*Epen*) has the form of a semi-circular flap, marked with a median groove, and closely resembling the corresponding structure in a lizard.

The optic thalami (fig 307, *Opt thal*) have the form of small rounded prominences projecting inwards from the lateral walls of the dorsal region of the diacœle (*di cœ.*), the remaining part of the wall of this cavity is still quite thin. Its roof is formed by a projecting sac-like velum interpositum (*vel int.*), which is apparently derived from the prepineal diverticulum of Stage A.

The long axis of the hemispheres (*Prosen*) is vertical instead of horizontal, and each shows a very distinct temporal lobe (fig 305). The corpus striatum (fig 304, *corp stri*) is very large, the mesial wall of the prosocœle (*pro s cœ*) quite thin.

#### *Stage G* (Plate 19, figs. 308 and 309)

This very interesting stage I was only able to examine from sections the figures are therefore restorations.

The hind-brain (*Meten*, *Epen*) has undergone comparatively little alteration, but the mid- and fore-brains show a condition of things as nearly as possible intermediate between Stage F and the adult.

The optencephals (*Opten*) have become widely separated from one another by the elongation of the optic commissure (*opt com*) or medio-dorsal portion of the mid-brain, they have therefore come to occupy a lateral position as in ordinary birds (see also Plate 12, fig 143). At the same time the hemispheres (*Prosen*) have grown backwards so as partly to cover the mid-brain. There is only wanted an increase in size, and forward extension of the cerebellum to convert the brain of *Apteryx* at this stage into a typical avian encephal.

#### *Stage H* (Plate 17, fig 310)

The adult characters are now fully attained, except that the optic lobes (*Opten.*) and the flocculi (*floc*) are considerably larger than in the fully developed organ.

### VIII.—THE EYE

(Plate 19, fig. 311)

I have only a single fact to mention with regard to the eye, but that is one of considerable interest. As OWEN showed, the pecten is absent in the adult, *Apteryx* being in this respect unique among birds. But in advanced embryos of stages H and I there is a distinct pecten in the form of a conical pigmented prominence, about 1–2 mm. long, passing from the entrance of the optic nerve towards the back of the lens. Figs 311 is taken from a dissection of Stage I fig 158 (Plate 13) shows its relations in a section of Stage H.

## SUMMARY

1. *New Terms Proposed*

*Chondrite*, an independent cartilaginous element, or centre of chondrification.

*Ostete*, an independent bony element or centre of ossification.

*Centrochondrite*, cartilaginous, *Centrostete*, bony, elements of a vertebral body

*Neurochondrite*, cartilaginous, *Neurostete*, bony, elements of a neural arch.

*Pleurochondrite*, cartilaginous, *Pleurostete*, bony, elements of a rib or autogenous transverse process

*Prochordal plate*, the middle trabecula of RATHKE, a mass of blastema formed above (cephalad of) the upturned anterior end of the notochord, and continuous behind with the parachordals

*Prochordal cartilage*, a nodular chondrite which appears in the prochordal plate, and gives rise to the medio-dorsal portion of the dorsum sellæ.

*Coraco-vertebral angle*, the angle enclosed between the long axis of the coracoid and that of the vertebral column

*Syn-sacrum*, the entire series of vertebræ which support the ilia, and include thoracic, lumbar, lumbo-sacral, sacral, and caudal vertebræ.

2. *External Characters.*

In Stage C, corresponding with a sixth day Chick, there is a well marked operculum growing backwards from the hyoidean fold, and covering the third (? and fourth) visceral cleft. A rudiment of this structure is seen in the preceding stage (pp. 30 and 31, Plate 3, figs 2, 3, and 4, Plate 5, fig 41)

In Stage A, corresponding in general features with a fourth day Chick, but in some respects not more advanced than one of the third day, the limbs have already attained their permanent position, so that if the backward shifting of the appendages so noticeable in the Chick occurs in *Apteryx*, it must take place at an unusually early period (p 28 ; Plate 3, fig. 1)

From the first appearance of the feather-papillæ there are well-marked pterylæ and apteria, most of which can be made out with tolerable distinctness in the adult (pp. 33, 34, and 35, Plate 3, figs. 8, 10, and 12).

The wing of the adult has a well-marked pre- and post-patagium, and amongst its feathers may be distinguished nine or ten cubitals, two or three metacarpals, one mid-digital, and a row of tectrices majores. The barbicels of the feathers are slightly curved (p. 37 ; Plate 3, figs. 14, 15, and 16).

The fore-limb passes through a stage in which it is a tridactyle paw with sub-equal digits, followed by one in which it is a typical wing with hypertrophied second and partially atrophied first and third digits (pp 32 and 33 ; Plate 3, figs. 6 and 9).

The nostril has acquired its final position at the end of the beak in Stage E : up to

the middle of incubation the whole respiratory region of the olfactory chamber from the anterior nares to the commencement of the turbinals, is filled with a solid mass of epithelial cells, through which a passage is formed at a later period (pp 61, 63, and 65, Plate 10, fig 114; Plate 10, fig 128, Plate 12, figs. 150 and 151) At no stage is there any trace of the caruncle or "egg-breaker" at the end of the beak (p 35)

### 3. *The Law of Growth.*

The head attains its maximum size in Stage F, *i.e.*, shortly before the appearance of ossification thereafter the beak increases, and the brain-case diminishes in relative size, the beak attaining its full proportional length in Stage H—probably about the middle of incubation—while the brain-case continues to undergo a relative diminution in size up to adult life (p 40, Plate 6 and Plate 7, fig 46)

The sternum and the pectoral and pelvic-girdles attain their maximum or nearly so in Stage F, thereafter undergoing but little alteration (pp. 40 and 42, Plate 6, and Plate 7, fig 47)

The fore-limb also attains its maximum proportional size in Stage F, undergoing little subsequent alteration (p. 42, Plate 6, and Plate 7, fig 48).

The hind-limb increases rapidly and regularly up to Stage K (time of hatching) between which period and the attainment of adult proportions there appears to be a slight decrease in relative length (p 42, Plate 6 and Plate 7, fig 49)

### 4 *Specific and Sexual Differences.*

The beak is relatively slightly longer in *A. australis* than in *A. oweni* the difference between the two sexes, in this respect, is very slight (p 40)

The pelvic girdle and the sternum are relatively longer in *A. australis* than in *A. oweni* the reverse appears to be the case with the scapula (p 42, Plate 7, fig 47)

The hind-limb is relatively longer in the male than in the female, the differences holding good for all three divisions of the leg There appear to be no constant specific differences in this respect (p 42; Plate 6 and Plate 7, fig 49)

In *A. australis* the alar claw is gently curved and of a light horn colour, blotched with black (p 37): the length of the corpus sterni, as defined on p 85, is greater than half its breadth, and the anterior margin of the sternum is concave, with an even curve (p. 85, Plate 16, figs 208 and 209) the manus has a carpo-metacarpus, but no free radiale or ulnare, and the third metacarpal is ossified from the second (pp. 92 and 97; Plate 17, fig 241, and Plate 18, figs 266 and 270)

In *A. oweni* the alar claw is soft and weak, gently curved, and of a light horn colour (p. 37). the length of the corpus sterni is less than half its breadth, and the anterior sternal margin is sinuous (p 85, Plate 16, figs 214 and 215) the manus has a free radiale in addition to the carpo-metacarpus, and the third metacarpal is ossified separately (pp. 93 and 98, Plate 17, figs. 242–244)

In *A. bulleri* the alar claw is black and strongly curved (p. 37) the length of the corpus sterni is less than half its breadth, and the anterior sternal margin is evenly curved and much more deeply emarginate than in *A. australis* (p. 85, Plate 16, figs 212 and 213) the manus is very variable, there is sometimes a simple carpo-metacarpus, sometimes a radiale and carpo-metacarpus, sometimes a radio-distale and free second and third metacarpals, sometimes the second metacarpal alone fuses with the carpals and sometimes with the distalia only, leaving a free radiale, the third metacarpal is, sometimes at least, ossified separately (pp. 93 and 97, Plate 17, figs 245-249, and Plate 18, fig. 268)

My observations on *A. haastii* are not sufficiently complete to have any systematic value

### 5 The Skull.

In Stages A and B the only cranial rudiments present are the parachordal plates, continued cephalad into the prochordal plate, and the visceral arches (pp. 56 and 57, Plate 4)

In Stage C the trabeculæ have appeared, and are continuous with the parachordals; the prochordal plate sends off paired processes directly upwards in the mesencephalic flexure, and laterad of the third nerves (pp. 57 and 58; Plate 5, figs. 35-37).

In Stages E and F the pituitary fossa is pierced by three apertures in longitudinal series—the anterior, middle, and posterior basicranial fontanelles. A theoretical explanation of these is given in fig. 103, Plate 10 (p. 60). The middle fontanelle has disappeared in Stage G (p. 63, Plate 11, fig. 126), but the anterior and posterior are still recognisable in Stages H and I (pp. 66 and 70; Plate 12, fig. 148; Plate 13, fig. 161, Plate 14, figs. 167, 173, and 174). Through the anterior fontanelle the pituitary pedicle passes.

The medio-dorsal portion of the dorsum sellæ arises as a distinct chondrite, the prochordal cartilage (pp. 62 and 64; Plate 10, figs. 109 and 111; Plate 11, fig. 126), which in Stages F and G is quite separate both from the trabecular and from the parachordal regions of the skull.

None of the stages show a separate prenasal cartilage or intertrabecula: if present as a distinct chondrite it certainly does not extend further backwards than the anterior presphenoidal region, the posterior presphenoidal region is clearly formed from the trabeculæ (p. 59, Plate 9, figs. 90 and 91).

In Stages D, E, and F the presphenoid is a vertical plate of considerable antero-posterior extent, and gives origin to a pair of large orbitosphenoids (pp. 59, 61, 62; Plate 9, figs. 85 and 86; Plate 10, figs. 96-98 and 104-108). In Stage G the orbitosphenoids have begun to atrophy (p. 64; Plate 11, figs. 123-126) and in later stages are reduced to narrow bars of cartilage (p. 47; Plate 9, fig. 75), the presphenoid at the same time undergoing a great diminution in antero-posterior extent.

The olfactory capsules extend backwards to the optic foramina mesiad of the eyes

(Plate 9, fig 77, and Plate 13, fig. 158) there is at no stage an interorbital septum

The turbinals are unusually well developed and are divisible into anterior, middle, posterior, anterior accessory, ventral accessory, and naso-turbinal folds. Alone amongst these the anterior accessory turbinal is formed as a hollow invagination of the wall of the olfactory capsule, not as a plate-like ingrowth (p 49, Plate 8, fig 57; Plate 9, figs. 83 and 84, Plate 12, fig 151, Plate 13, figs 153-158) its cavity contains a prolongation of the antrum of HIGHMORE

These are paired, rod-like, JACOBSON'S cartilages, lying one on each side of the rostrum in the vomerine region (p 51, Plate 9, figs 76 and 77, Plate 13, figs. 155-157).

In late embryonic life, and even in the adult, the quadrate articulates with the roof of the tympanic cavity by a double articular surface (p 51, Plate 9, figs 78 and 79)

The hyoidean portion of the tongue-bone chondrifies late—subsequently to Stage G—and never ossifies (pp. 52 and 65, Plate 9, fig 82, and Plate 11, fig. 132)

## 6 *The Vertebral Column.*

As in other Birds, the atlas arises from a post-occipital intercentrum and a pair of neurochondrites. The axis consists originally of seven pieces, its own centrochondrite, the odontoid or centrochondrite of the atlas, a post-atlantal intercentrum, a pair of neurochondrites, and a pair of pleurochondrites. In both vertebræ each of these elements ossifies separately (pp 73 and 79, Plate 15, figs 175-179 and 194)

The way in which the notochord is constricted by the ingrowing centrochondrites differs greatly in the various regions (p 79, Plate 15, figs 194-197)

The atlas and axis in a newly-hatched embryo differ far less than in the adult from those of the other Ratitæ (p 73)

Two intercentra are described in the caudal region (pp. 78 and 84, Plate 15, figs 188 and 206)

A new method of writing the vertebral formula of Birds is adopted (pp 78, 81, and 83)

## 7 *The Sternum and Ribs*

In Stage E the sternum is nearly horizontal in position, only two sternal ribs are attached to it by joints, and a third by indifferent tissue, and it does not extend caudad of the attachment of the third (p. 87, Plate 16, fig 216). In Stage F three ribs are united to it by joints, and a fourth by fibrous tissue (p. 87, Plate 16, fig. 217). In Stage G there is the normal number of four sternal ribs in connection with the sternum. These facts seem to show that the costal sternum does not originate by the union of the ventral ends of all four sternal ribs, but that it extends backwards independently of the third and fourth ribs, meeting them in turn and becoming united with them by joints

In some adult specimens the sternum bears a low median ridge, probably to be looked upon as a vestigial keel (p. 86 ; Plate 16, figs 210, 211, and 213).

The form of the adult sternum is very variable (Plate 16, figs 208-215).

### 8 *The Shoulder-Girdle*

Up to Stage H the shoulder girdle is a single cartilage (Plate 17, figs. 233-237). During that stage the procoracoid and coracoid are differentiated by fenestration (p. 91, Plate 17, fig. 238). The procoracoid degenerates into a ligament (p. 92, Plate 17, figs. 239 and 240), which is sometimes present in the adult (p. 89, Plate 16, figs 225, 226, and 229). The coracoid fenestra may persist or may be filled up by a preaxial extension of the coracoid (p. 89 ; Plate 16, figs 225-232).

Acromial, procoracoid, and acrocoracoid tuberosities are present (p. 90 ; Plate 16, figs 225-232).

The coraco-scapular angle varies from  $150^{\circ}$  to  $122^{\circ}$ . In Stage E the scapula is curved backwards over the ribs (p. 91, Plate 16, fig. 216). In the same stage the coraco-vertebral angle is  $35^{\circ}$ , by Stage H it has increased to  $90^{\circ}$  (p. 91).

The adult shoulder-girdle is subject to great variation both in form and size (Plate 16, figs 225-232).

### 9. *The Fore-Limb.*

In the carpus a radiale, an ulnare, and the three preaxial distalia are distinguishable in early stages (pp. 94-95 ; Plate 17, figs. 254-260). The distalia usually conalesce with the second and third metacarpals to form a carpo-metacarpus, with which the radiale and ulnare may or may not become united (pp. 95-97 ; Plate 17, figs. 261-264, and Plate 18, figs 265-273).

The pollex usually atrophies at an early stage, but a vestige of it may persist (pp. 95 and 97 ; Plate 17, figs 257 and 263 ; Plate 18, fig. 271).

The manus is fairly constant in structure in *A. australis* and *A. oweni*, but is very variable in *A. bulleri* (p. 92, Plate 17, figs. 241-253).

### 10 *The Pelvic-Girdle.*

The pubis and ischium are nearly vertical in Stages D and E, and gradually become rotated backwards (pp. 98 and 99 ; Plate 18, figs. 274-277).

The post-ilium is already fully formed in Stage D, the pre-ilium not until Stage G (pp. 98 and 99 ; Plate 18, figs. 274-277).

The pectineal process is ossified equally from the ilium and the pubis (p. 99 ; Plate 18, fig. 279).

11 *The Hind-Limb*

In the tarsus a tibiale, a fibulare, and a single distale are distinguishable in Stages D and E (p. 101, Plate 18, figs 280 and 283). In F a postaxial centrale appears in the rudiment of the mesotarsal articular pad (p. 101, fig. 287), in G it becomes chondrified (p. 102, fig. 291), and in the adult ossified (p. 100, fig. 292). A smaller preaxial centrale is first seen as a distinct chondrite in Stage L (p. 102); in the adult of *A. australis* and *A. haastii* (?) it was observed as a separate bone in the preaxial moiety of the mesotarsal pad (p. 100, fig. 292).

In Stage D the fifth digit is represented by an elongated metatarsal (p. 101, fig. 282), in E this has diminished in size (p. 101; fig. 284), and in F undergone almost complete atrophy (p. 102; fig. 288).

12. *Muscles of the Wing.*

The following muscles are present in the wing in addition to those described by OWEN —Brachialis anticus, supinator, pronator, anconeus, flexor profundus internus, extensor carpi ulnaris, extensor metacarpi radialis brevis, extensor indicis proprius, and flexor digitorum profundus. There may also be a brachialis anticus accessorius, an interosseus dorsalis, and probably a flexor carpi radialis (p. 104; Plate 19, figs. 293-296).

The biceps arises from the acrocoracoid, the triceps by a long head from the scapula and by a short head from the humerus (p. 104, fig. 293).

13. *The Brain.*

The mesencephal is unusually small from the first (p. 108, Plate 3, figs 1 and 2). In Stages D-F the optic lobes are dorsal (Plate 19, figs 304 and 306), in G they become lateral by the transverse extension of the optic commissure or median portion of the roof of the mesocoele (p. 109, figs 308 and 309); in H they are already ventral, although larger proportionally than in the adult (fig. 310).

The diencephal becomes tilted backwards in later stages, its dorsal wall becoming posterior, and the foramen of MONRO postero-dorsal instead of antero-dorsal (p. 106; fig. 301).

The anterior commissure and corpus callosum are large (fig. 301).

The cerebral hemispheres are of unusual proportional length, and partly cover the cerebellum (figs. 297, 299, and 301).

14. *The Eye*

A pecten is present during late embryonic life (p. 109, Plate 13, fig. 158, and Plate 19, fig. 311).



15 *Phylogeny.*

The following characters support the view that *Apteryx* is derived from a typical Avian form capable of flight —

- a* The presence of an alar membrane or patagium (p 36 ; Plate 3, figs. 14 and 15)
- b* The presence of pterylæ and apteria (pp 33, 34, and 35 , Plate 3, figs. 8, 10, and 12)
- c* The presence of remiges and of tectrices majores (p 37 , Plate 3, figs. 14 and 15).
- d* The attitude assumed during sleep (p 36)
- e* The presence of two articular facets on the head of the quadrate (p. 51).
- f* The presence of a pygostyle (p 83)
- g* The extreme variability of the sternum, shoulder-girdle, and wing, indicating degeneration. \*
- h* The occasional occurrence of a median longitudinal ridge or vestigial keel on the sternum (Plate 16, figs. 210, 211, and 213).
- i* The position of the shoulder-girdle and sternum in Stage E (p. 91 , Plate 16, fig. 216).
- j* The presence of vestigial acromial, procoracoid, and acrocoracoid processes.
- k* The fact that the skeleton of the fore-limb is that of a true wing in Stage F (p. 94 ; Plate 17, fig. 256)
- l* The early assumption of undoubted avian characters in the pelvis (p. 98).
- m* The typically avian characters, both as to structure and development, of the vertebral column and hind-limb.
- n* The fact that the brain passes through a typical avian stage with lateral optic lobes (p. 109 , Plate 19, figs. 308 and 309).
- o* The relations of the subclavius muscle (p. 90 ; Plate 19, fig. 293)

On the other hand the total absence of rectrices tells against this view.

The following characters indicate derivation from a more generalised type than existing Birds —

- a* The characters of the chondrocranium, especially in the earlier stages (pp. 59, &c.). Many of these peculiarities, *e g.*, the absence of an interorbital septum, may, however, be adaptive and correlated with the diminished eyes and the enlarged olfactory organs.
- b* The presence of an operculum in early stages (pp. 30 and 31 ; Plate 3, figs. 2, 3, and 4 , Plate 5, fig. 41). As however this structure has not been described in Reptiles, it either proves nothing or too much.
- c* The presence of a well-marked procoracoid in comparatively late embryonic life (p. 92 ; Plate 17, figs 238 and 239).
- d* The characters of the pelvis

On the other hand, in the following characters *Apteryx* exhibits greater specialisation than other birds —

- a The early assumption of their permanent position by the limbs (p 29)
- b The late appearance and obviously degraded character of the hyoid portion of the tongue-bone (pp 52 and 65)
- c The position of the nostrils and the peculiar mode of development of the respiratory section of the nasal chamber (pp. 61, 63, and 65)
- d. The total absence of clavicles.

Such characters as the position of the basipterygoid processes, the broad vomer, and the presence of JACOBSON'S cartilages, being paralleled in existing Carinatae, some of them even in Passerines, can hardly be considered as of fundamental importance, since they may be derived either from a Proto-Carinate or from an early typical Carinate stock.

Before considering the peculiarities in the development of the sternum as of fundamental importance, it will be necessary to study that of the flightless Carinatae, and especially of *Stringops* (p 86)

The general balance of evidence seems to point to the derivation of both Ratitae and Carinatae from an early group of typical flying Birds, or *Proto-Carnatae* (p 37)

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\* The so-called "Preliminary Note on the Development of the Skeleton of the *Apteryx*," is merely an unrevised extract from my rough note book, and was not intended for publication. I am, also, not

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responsible for the figures in the actual (so-called Second) Preliminary Note, which have the sizes incorrectly given

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## DESCRIPTION OF PLATES 3-19

The scale of enlargement is given on the figures themselves

In plates dealing with the skeleton cartilaginous parts are coloured green and cartilage bones brown, membrane bones are uncoloured or (in sections) black, prochondral tissue is darkly shaded.

## A. EXTERNAL FORM.

*References.*

<i>All.</i>	Allantois (in outline)	<i>Mes.Som.</i> 16 and 28.	16th and 28th mesoblastic somites.
<i>Au.</i>	Auditory sac	<i>Meten</i>	Metencephal.
<i>Claw</i>	Terminal claw of wing.	<i>Mid.dig.</i>	Mid-digital remex.
<i>Olo Ap.</i>	Cloacal aperture	<i>Mn.</i>	Mandibular fold.
<i>Cl.</i> 1-4	Visceral clefts.	<i>Mtcp.</i>	Metacarpal remiges.
<i>Cubit 1</i>	First cubital remex.	<i>Mth.</i>	Mouth.
<i>Dien</i>	Diencephal	<i>Na.</i>	External nasal aperture.
<i>Dors Pt</i>	Dorsal pteryla	<i>Nch.</i>	Notochord.
<i>Fem.Pt.</i>	Femoral pteryla	<i>Operc.</i>	Operculum.
<i>F L.</i>	Fore-limb	<i>Prosen.</i>	Prosencephal.
<i>Fr Na P.</i>	Fronto-nasal process	<i>Pr.Ptgm.</i>	Pre-patagium.
<i>H L.</i>	Hind-limb	<i>Pt.Ptgm.</i>	Post-patagium.
<i>Ht</i>	Heart	<i>S.Ma.P.</i>	Superior maxillary process.
<i>Hum Pt.</i>	Humeral pteryla.	<i>Som.Stk.</i>	Somatic stalk
<i>Hy</i>	Hyoid fold.	<i>Tect.maj.</i>	Tectrices majores.
<i>Inf.Al Apt</i>	Lower wing space.	<i>Upg.</i>	Uropygium.
<i>Lat Apt</i>	Lateral apterium.	<i>Vent.Apt</i>	Ventral apterium
<i>Mesen.</i>	Mesencephal	1-4	Digits of manus or pes.

Plate	Fig	Stage	Species	
3	1	A	<i>australis</i>	Entire embryo from the right side
	2	B	"	" " " " "
	3	C	"	" " " left "
	4	"	"	The head, obliquely from beneath
	5	D	<i>oweni</i>	Entire embryo from the left side The heart is exposed by rupture of the body wall
	6	E	"	Entire embryo from the left side Heart exposed by rupture of body wall
	7	"	"	Pes, dorsal aspect
	8	F	"	Entire embryo from the left side
	9	"	"	Fore-limb, dorsal (external) aspect
	10	G	<i>australis</i>	Entire embryo from the right side
	11	"	"	Caudal extremity
	12	I	"	Embryo from the left side with the feathers removed
	13	"	"	Left wing, ventral (inner) aspect
	14	Adult	<i>bulleri</i>	Right wing, dorsal (outer) aspect
	15	"	"	" " ventral (inner) "
	16	"	"	Barbule of a wing-feather, showing curved barbicels

## B. SECTIONS OF STAGES A, B, AND C

## References

<i>Au</i>	Auditory capsule	<i>Jug V</i>	Jugular vein
<i>Au C</i>	Auditory capsule	<i>Mes neph</i>	Mesonephros
<i>Aula</i>	Cavity of basi-cerebrum	<i>Lam ter m</i>	Lamina terminalis
<i>Bas Art</i>	Basilar artery	<i>Mn</i>	Mandibular fold
<i>Bas Orb</i>	Basi-cerebrum, or median portion of secondary fore-brain	<i>M Pl</i>	Muscle plate
<i>Bs Opt</i>	Basi-opticus, or mid-ventral portion of mid-brain	<i>Ms cœ</i>	Mesocœle (cavity of mid-brain)
<i>Br 1-3</i>	Branchial folds.	<i>Mt cœ</i>	Metacœle (4th ventricle)
<i>Cent</i>	Rudiment of centrum	<i>Mth</i>	Mouth
<i>Cl 1-5</i>	Visceral clefts.	<i>My</i>	Myelon
<i>Cl Ap</i>	Cloacal aperture	<i>Na</i>	Nasal sac
<i>Cœl</i>	Cœlome	<i>Nch</i>	Notochord
<i>D Ao</i>	Dorsal aorta	<i>Nv 3, 5, 10</i>	Oculomotor, trigeminal, and vagus nerves
<i>Di Cœ</i>	Diacœle (3rd ventricle)	<i>Oper c</i>	Operculum
<i>Epen.</i>	Epencephal (cerebellum)	<i>Opt cœ</i>	Optocœle (cavity of optic lobe)
<i>f</i>	Fissure between mesoblastic somites	<i>Opten</i>	Optencephal (optic lobe)
<i>F L.</i>	Fore-limb	<i>Opt ves</i>	Primary optic vesicle
<i>For Monro</i>	Foramen of MONRO	<i>Pa Ch</i>	Parachordal plate
<i>Fr Na P</i>	Fronto-nasal process	<i>Pm</i>	Pineal body
<i>H L.</i>	Hind-limb	<i>Pr Ch</i>	Prochordal plate
<i>Hy</i>	Hyoid fold	<i>Pr Pin Divert</i>	Pre-pineal diverticulum
<i>Inf</i>	Infundibulum.	<i>Ps cœ</i>	Prosocœle (lateral ventricle)
<i>Int Car</i>	Internal carotid.	<i>Pty</i>	Pituitary body
<i>Iten</i>	Iter a tertio ad quartum ventriculum	<i>S Mx P</i>	Superior maxillary process
		<i>Sp Gn</i>	Spinal ganglion
		<i>Tr</i>	Trabecula
		<i>V Ao</i>	Ventral aorta

Plate	Fig	Stage	Species	
4	17	A	<i>australis</i>	Sagittal section of head through median plane
	18	"	"	Pineal region of same section enlarged
	19	"	"	Part of 20th section laterad of median plane
	20	"	"	" 30th " " "
	21	"	"	" 40th " " "
	22	B	"	Horizontal section of head, level of diacole
	23	"	"	" " " " eyes
	24	"	"	" " " " pituitary body
	25	"	"	" " " " nasal aperture
	26	"	"	Transverse " " " mandibular fold
	27	"	"	" " " " hyoid fold
	28	"	"	" " " " operculum
	29	"	"	" " " " 2nd visceral cleft
	30	"	"	" " " " 3rd visceral cleft
	31	"	"	" " " trunk " fore limbs
	32	"	"	" " " " hind-limbs
	33	"	"	Horizontal " " " notochord
5	34	C	"	" " " head " diacole
	35	"	"	" " " " eyes
	36	"	"	" " " " "
	37	"	"	Transverse " " " superior maxillary process
	38	"	"	" " " " mandibular fold
	39	"	"	" " " " hyoid fold
	40	"	"	" " " " "
	41	"	"	" " " " operculum and 2nd
	42	"	"	" " " " " " 3rd visceral cleft
	43	"	"	" " " trunk " hind-limbs
	44	"	"	Horizontal " " " notochord

## C. GRAPHIC REPRESENTATIONS OF RATE OF GROWTH.

Plate	Fig	
6	45	Diagram showing the relative dimensions of various regions of the body in the different stages, the length of the vertebral column being taken as a standard
7	46	Diagram showing curve of growth of the entire head, the brain case, and the beak, expressed as percentages of the vertebral column
	47	Diagram showing curves of growth of the ilium, sternum, scapula, and coracoid: vertebral column = 100
	48	Diagram showing curves of growth of entire fore-limb, brachium, antebrachium, and manus vertebral column = 100
	49	Diagram showing curve of growth of entire hind-limb, femur, crus, tarso-meta tarsus, and third digit. vertebral column = 100



## D THE SKULL

## References

<i>a</i>	Process of ectoethmoid	<i>Inf</i>	Infundibulum
<i>A A Trb</i>	Anterior accessory turbinal	<i>I St</i>	Infra-stapedial
<i>a bcr fo</i>	Anterior basicranial fontanelle	<i>Ja C</i>	JACOBSON'S cartilage
<i>A Trb</i>	Anterior turbinal	<i>Ju</i>	Jugal
<i>Al Sph</i>	Alisphenoid	<i>ju pr</i>	Jugal process of maxilla.
<i>Ang</i>	Angular	<i>Lac</i>	Lacrymal
<i>Ant Hgh</i>	Antium of HIGHMORE	<i>Lac D</i>	Lacrymal duct
<i>Ant Na</i>	Anterior nares	<i>Lac Gl</i>	Lacrymal gland
<i>Art</i>	Articular	<i>lac for</i>	Lacrymal foramen
<i>Aiy</i>	Aiytenoid cartilage	<i>m bcr fo</i>	Middle basicranial fontanelle
<i>A S C</i>	Anterior semicircular canal	<i>Mck C</i>	MCKEL'S cartilage
<i>Au C</i>	Auditory capsule	<i>M Eth</i>	Mesethmoid
<i>Bas Art</i>	Basilar artery	<i>M Pter</i>	Pterygoid muscle
<i>B Br</i>	Basibranchial	<i>M Temp</i>	Temporal muscle
<i>B Hy</i>	Basihyal	<i>Mth</i>	Mouth
<i>B Oc</i>	Basioccipital	<i>M Trb</i>	Middle turbinal
<i>B pty pr</i>	Basipterygoid process	<i>Mr</i>	Maxilla
<i>b pty pr</i>	Facet on pterygoid for articulation of ditto	<i>Na</i>	Nasal
<i>B. Sph</i>	Basisphenoid	<i>na</i>	Foramen for nutrient artery
<i>B Temp</i>	Basitemporal	<i>na pr</i>	Nasal process of premaxilla or of frontal
<i>C Br</i>	Cerato-branchial	<i>Na Trb</i>	Naso-turbinal
<i>C Hy</i>	Cerato-hyal	<i>Nch</i>	Notochord
<i>C Hy'</i>	Prochondral rudiment of ditto	<i>Nv I-XII</i>	Cerebral nerves or their foramina
<i>Cn 1 and 2</i>	Internal and external condyles of quadrate	<i>Nv V<sup>1-3</sup></i>	The three divisions of the tri- geminal or their foramina
<i>Col</i>	Columella auris	<i>Nv V<sup>1 a and b</sup></i>	The two rami of the orbito-nasal nerve
<i>Cor</i>	Coronary	<i>Oc cn</i>	Occipital condyle
<i>Op Str</i>	Corpus striatum	<i>Oc for</i>	Occipital foramen
<i>cr fa c</i>	Craniofacial cavity	<i>Olf fos</i>	Olfactory fossa
<i>Dent</i>	Dentary	<i>Olf sac</i>	Olfactory sac
<i>Dent'</i>	Fibrous rudiment of ditto	<i>Op Ot</i>	Opisthotic
<i>Di cæ</i>	Diacæle (3rd ventricle)	<i>orb pr</i>	Orbital process of frontal or of quadrate
<i>Dors sell</i>	Dorsum sellæ	<i>Orb Sph</i>	Orbito-sphenoid
<i>d pr.</i>	Descending process of nasal or of frontal	<i>o sph pr</i>	Orbito-sphenoid process of frontal
<i>E Br</i>	Epibranchial	<i>ot pr</i>	Otic process of quadrate
<i>Ec Eth 1-5</i>	The five regions of the ecto- ethmoid	<i>Pa</i>	Parietal
<i>E St</i>	Extra-stapedial	<i>Pa Ch</i>	Parachordal cartilage
<i>Eth Pr Sph</i>	Ethmo-presphenoid bone	<i>Pal</i>	Palatine
<i>Eus T</i>	Eustachian tube or its bony canal	<i>pal pr</i>	Palatine process of premaxilla or of maxilla
<i>Ex Col</i>	Extra-columella	<i>pa oc pr</i>	Paroccipital process
<i>Ex oc</i>	Exoccipital	<i>p bcr fo</i>	Posterior basicranial fontanelle
<i>Ext Aud M</i>	External auditory meatus	<i>Pect</i>	Pecten
<i>flc f</i>	Floccular fossa	<i>Pmx</i>	Premaxilla
<i>fov</i>	Fenestra ovalis	<i>Pmx'</i>	Fibrous rudiment of ditto
<i>Fr</i>	Frontal	<i>pn c</i>	Pneumatic cavity
<i>f rot</i>	Fenestra rotunda	<i>pn f</i>	Pneumatic foramen
<i>H S.C</i>	Horizontal semicircular canal	<i>Pr Ch</i>	Prochordal cartilage
<i>Int. Car.</i>	Internal carotid or its foramen.		

<i>P<sub>1</sub> Na</i>	Prenasal cartilage	<i>Rost</i>	Rostrum.
<i>Pr Ot</i>	Prootic	<i>S Ang</i>	Supra-angular
<i>pr ot</i>	Facet on head of quadrate for articulation with ditto	<i>Scl</i>	Sclerotic
<i>P<sub>1</sub> osen</i>	Piosencephal	<i>S Oc</i>	Supra-occipital.
<i>P<sub>1</sub> s cæ</i>	Prosocœle (lateral ventricle)	<i>S orb F</i>	Superior orbital fontanelle.
<i>P<sub>1</sub> Sph</i>	Piesphenoid	<i>Spl</i>	Splenic
<i>P<sub>1</sub> Sph'</i>	Paired moieties of ditto in Stage D	<i>S St</i>	Supra-stapedial.
<i>P<sub>1</sub> Tmp</i>	Pretemporal wings	<i>Sq</i>	Squamosal
<i>Ptg</i>	Pterygoid	<i>Sq'</i>	Fibrous rudiment of ditto.
<i>Ptg'</i>	Fibrous rudiment of ditto	<i>sq</i>	Facet for ditto on head of quadrate
<i>Pt Na</i>	Posterior nares	<i>tq p<sub>1</sub></i>	Tegminal process
<i>P T<sub>1</sub> b</i>	Posterior turbinals	<i>Thy</i>	Thyroid cartilage
<i>Pty</i>	Pituitary body	<i>Tr</i>	Trabecula.
<i>Pty, F</i>	Pituitary fossa	<i>Tr ch</i>	Trachea
<i>Pty ped</i>	Pituitary pedicle	<i>Tymp. C.</i>	Tympanic cavity.
<i>Qu</i>	Quadrate	<i>Tymp M</i>	Tympanic membrane
<i>Qu (orb pr)</i>	Orbital process of ditto	<i>V A T<sub>1</sub> b</i>	Ventral accessory turbinal
<i>Qu (ot p<sub>1</sub>)</i>	Otic process of ditto	<i>Vo</i>	Vomer.
<i>qu</i>	Facet for articulation of ditto on pterygoid or on quadrate-jugal	<i>æ.</i>	Transverse commissure between trabecula, separating anterior and middle basi-cranial fontanelles.
<i>qu<sup>1</sup></i>	Ditto on prootic.	<i>y.</i>	Ditto between parachordals, separating middle and posterior basi-cranial fontanelles.
<i>qu<sup>2</sup></i>	Ditto on alisphenoid		
<i>qu<sup>3</sup></i>	Ditto on squamosal		
<i>Qu Ju</i>	Quadrato-jugal.		
<i>Qu Ju'</i>	Fibrous rudiment of ditto		
<i>r</i>	Ridge of parachordal.	<i>zyg p<sub>1</sub>.</i>	Zygomatic process of squamosal.
<i>Rhinen</i>	Rhinencephal		

Plate	Fig	Stage.	Species	
8	50	K	<i>bulleri</i>	Entire skull, dorsal aspect
	51	"	"	" " ventral "
	52	"	"	" " from left side
	53	"	"	" " " behind
	54	"	"	Mandible, dorsal
	55	"	"	" ventral
	56	"	"	Entire skull, sagittal section
	57	"	"	The turbinals of the right side, mesial aspect, exposed by removal of mesethmoid
	58	"	<i>australis</i>	The separate membrane bones
	to 74			
9	75	"	"	Chondrocranium, dorsal
	76	"	"	" ventral
	77	"	"	" left side
	78	"	"	Dorsal wall of tympanic cavity

Plate	Fig	Stage	Species.	
9	79	K	<i>austrials</i>	Quadiate, mesial aspect
	80	"	"	Mandible after removal of membrane bones, ventral
	81	"	"	Columella auris, posterior aspect
	82	"	"	Tongue bone, dorsal
	83	"	"	Horizontal section of turbinals
	84	"	"	" " " further ventrad
	85	D	<i>owen</i>	Entire skull, left side
	86	"	"	Chondrocranium, sagittal section
	87	"	"	Columella auris
	88	"	"	Transverse section of head, anterior olfactory region
	89	"	"	" " " level of posterior nares
	90	"	"	" " " eyes
	91	"	"	" " " optic nerves
	92	"	"	" " " basipterygoid processes
	93	"	"	" " " pituitary pedicle
	94 } 95 }	"	"	" " " parachordals
10	96	E	"	Entire skull from left side, restored from sections
	97	"	"	Chondrocranium, dorsal, from a dissection
	98	"	"	" sagittal section, restored from sections
	99	"	"	Columella auris, restored from sections
	100	"	"	Sagittal section of head, through olfactory chamber
	101	"	"	Median sagittal section through basis crani
	102	"	"	Sagittal section of ditto, slightly laterad of median plane
	103	"	"	Diagram of basis crani from above, showing probable relations of parachordals and trabeculae
	104	F	"	Entire skull, from left side, from a dissection
	105	"	"	Chondrocranium, dorsal " "
	106	"	"	" ventral " "
	107	"	"	" from left side " "
	108	"	"	" sagittal section, restored from previous dissections and from sections
	109	"	"	Pituitary region of ditto, with connective tissue removed
	110	"	"	Tongue-cartilage (first branchial arch)
	111	"	"	Median sagittal section of basis crani
	112	"	"	Sagittal section of basis crani, 0.2 mm laterad of median plane
	113	"	"	Transverse section of head, anterior olfactory region
	114	"	"	" " " part of ditto, showing characters of olfactory sac
	115	"	"	" " " anterior turbinal region
	116	"	"	" " " presphenoidal region
	117	"	"	" " " level of basipterygoid processes
	118	"	"	" " " dorsum sellae
	119	"	"	" " " tympanic cavity

Plate	Fig	Stage	Species	
11	120	G	<i>owenii</i>	Entire skull, dorsal
	121	"	"	" " ventral
	122	"	"	" " left side
	123	"	"	Chondrocranium, dorsal
	124	"	"	" " ventral
	125	"	"	" " left side
	126	"	"	" " sagittal section
	127	"	<i>australis</i>	Transverse section of head, anterior end of beak
	128	"	"	" " " level of anterior nares
	129	"	"	" " " naso-turbinal
	130	"	"	" " mandible slightly caudad of preceding
	131	"	"	" " head, anterior turbinal region
	132	"	"	" " " level of posterior nares
	133	"	"	" " " eyes
	134	"	"	" " " pituitary pedicle
	135	"	"	" " " anterior basiscranial fontanelle
	136	"	"	" " " optic nerves and basiptyergoid processes
	137	"	"	" " " pituitary body and internal carotid foramen
12	138	"	"	" " " just caudad of pituitary body
	139	"	"	" " " level of dorsum sellae
	140	"	"	" " " posterior basiscranial fontanelle
	141	"	"	" " " trigeminal foramen
	142	"	"	" " " tympanic cavity
	143	"	"	" " " condyloid foramen
	144	"	"	" " " occipital foramen
	145	"	"	" " " posterior end of auditory capsule
	146	H	<i>bulleri</i>	Entire skull, dorsal
	147	"	"	Portion of chondrocranium, dorsal
	148	"	"	" " " ventral
13	149	"	<i>owenii</i>	Transverse section of head, anterior end of beak
	150	"	"	" " " level of anterior nares
	151	"	"	" " " naso turbinal
	152	"	"	" " " at junction of first and second portions of ectoethmoid
	153 }	"	"	" " " region of ventral accessory turbinal
	154 }	"	"	" " " " and anterior accessory turbinals
	155 }	"	"	" " " " " "
	156 }	"	"	" " " " " "
	157	"	"	" " " " " anterior and middle turbinals
	158	"	"	" " " " " level of eye
	159	"	"	" " " " " presphenoid region
	160	"	"	" " " " " anterior part of pituitary fossa

Plate	Fig	Stage	Species	
13	161	H	<i>owen</i>	Transverse section of head, level of anterior basicranial fontanelle
14	162	"	"	" " " posterior part of pituitary fossa
	163			
	164	"	"	" " " through dorsum sellæ
	165			
	166			
	167	"	"	" " " posterior basicranial fontanelle
	168			
	169	"	"	" " " level of tympanic cavity
	170			
	171	"	"	" " " occipital condyle
	172	I	<i>australis</i>	Chondrocranium, dorsal
	173	"	"	Sagittal section through basis cranii
	174	"	<i>bulleri</i>	" " " "

## E VERTEBRAL COLUMN AND RIBS

*References*

<i>azyg</i>	Anterior zygapophysis	<i>neu</i>	Neuroid
<i>capit</i>	Head of rib	<i>n ost</i>	Neurosteite
<i>chn</i>	Centrochondrite	<i>n sp</i>	Neural spine
<i>Cd</i>	Caudal vertebræ *	<i>Oc cn</i>	Occipital condyle
<i>Cor</i>	Coracoid	<i>Od</i>	Odontoid
<i>O ost</i>	Centrosteite	<i>parap</i>	Parapophysis
<i>Cv Th Rb</i>	Rib of cervico-thoracic vertebra	<i>pl</i>	Pleuroid
<i>diap</i>	Diapophysis	<i>pl chn</i>	Pleurochondrite
<i>Fe</i>	Femur	<i>pl ost</i>	Pleurosteite
<i>Il</i>	Ilium	<i>pt atl int c</i>	Post-atlantal intercentrum
<i>int cent</i>	Intercentrum	<i>pt oc int c</i>	" occipital "
<i>int vert for</i>	Intervertebral foramen	<i>Pu</i>	Pubis
<i>Isch</i>	Ischium	<i>Pyg</i>	Pygostyle
<i>Lb.</i>	Lumbar vertebræ	<i>Sc</i>	Sacral vertebræ
<i>Lb Sc</i>	Lumbo-sacral vertebræ	<i>Scap</i>	Scapula
<i>lg</i>	Ligament	<i>St</i>	Sternum
<i>My</i>	Myelon	<i>Th</i>	Thoracic vertebræ
<i>Nch</i>	Notochord.	<i>tuberc</i>	Tubercle of rib
<i>n c su</i>	Neurocentral suture	<i>Unc</i>	Uncinates

\* These and the remaining vertebræ are numbered in order, the numbers in brackets give the position in the entire series.

PROFESSOR T. J. PARKER ON THE ANATOMY

Plate	Fig	Stage	Species	
15	175	K	<i>australis</i>	Atlas, cephalic aspect
	176	"	"	" caudal "
	177	"	"	Axis, left side
	178	"	"	" ventral
	179	"	"	" sagittal section
	180	"	"	3rd cervical, dorsal aspect
	181	"	"	5th " anterior aspect
	182	"	"	" " posterior "
	183	"	"	Cervico-thoracic, anterior aspect
	184	"	"	1st thoracic "
	185	"	"	2nd " "
	186	"	"	Syn-sacrum and caudal vertebræ, left side
	187	"	"	" " " ventral
	188	"	"	Last four caudal vertebræ, left side
	189	"	"	" " dorsal
	190	"	<i>bulleri</i>	Caudal vertebræ, left side
	191	D	<i>owen</i>	Vertical section of 12th cervical vertebræ
	192	"	"	" " 3rd thoracic "
	193	"	"	" " 1st sacral "
	194	E	"	Sagittal section of anterior cervical region, median
	195	"	"	" " " " " laterad of mesial plane
	196	"	"	" " sacral region
	197	"	"	" " posterior caudal region
	198	G	"	Atlas, anterior
	199	"	"	Axis "
	200	"	"	" left side
	201	"	"	Thoracic vertebra, anterior
	202	"	<i>australis</i>	1st sacral vertebra
	203	"	"	Posterior caudal vertebræ } Restored from sections
	204	I	"	Post-cervical portion of vertebral column, with ribs, sternum, shoulder-girdle, and pelvis, left side
	205	O	<i>owen</i>	Syn-sacrum, left side
	206	Adult	<i>australis</i>	Posterior caudal region, right side
	207	"	<i>owen</i>	" " " sagittal section

## F THE STERNUM

## References

<i>ant lat pr</i>	Anterior lateral process	<i>Pl ost</i>	Pleurostemon
<i>Cor</i>	Coracoid	<i>post lat pr</i>	Posterior lateral process
<i>Cor gn</i>	Coracoid groove	<i>post med pr</i>	„ median „
<i>Cv Th Rb</i>	Cervico-thoracic rib	<i>Scap</i>	Scapula
<i>fo</i>	Fontanelle	<i>St</i>	Sternum
<i>Hu</i>	Humerus	<i>Th Rb , 1-4</i>	Thoracic ribs
<i>k</i>	Median ridge or vestigial keel	<i>Unc</i>	Uncinates

Plate	Fig	Stage	Species	
16	208	Adult	<i>australis</i>	Sternum, ventral
	209	„	„	„ „
	210	„	<i>haastii ?</i>	„ „
	211	„	<i>maxima</i> = <i>bulleri</i>	„ „
	212	„	<i>bulleri</i>	„ „
	213	„	„	„ „
	214	„	<i>owenii</i>	„ „
	215	„	„	„ „
	216	E	„	„ with shoulder-girdle, anterior ribs, &c , left side
	217	F	„	„ with anterior ribs, left side
	218	G	<i>australis</i>	„ ventral
	219	„	„	„ transverse section
	220	H	<i>bulleri</i>	„ ventral
	221	„	<i>owenii</i>	„ „
	222	K	<i>australis</i>	„ „
	223	L	„	„ „
	224	M	<i>owenii</i>	„ „



## G. THE SHOULDER-GIRDLE

## References

<i>ac</i>	Acromial tuberosity	<i>Pr cor</i>	Procoracoid
<i>acr cor</i>	Acrocoracoid tuberosity	<i>pi cor t</i>	Piocracoid tuberosity
<i>Cor</i>	Coracoid	<i>pr cor lg</i>	,, ligament
<i>Cor fen</i>	Coracoid fenestra	<i>Scap</i>	Scapula
<i>gl</i>	Glenoid cavity	<i>Sup cor for</i>	Supracoracoid foramen

Plate	Fig	Stage	Species						
16	225	Adult	<i>maxima</i> <i>=bulleri</i>	Shoulder-girdle	A ventral, B. lateral aspect				
	226	„	<i>haastri</i> ?	„	„	„	„	„	„
	227	„	<i>australis</i>	„	„	„	„	„	„
	228	„	„	„	„	„	„	„	„
	229	„	<i>bulleri</i>	„	„	„	„	„	„
	230	„	„	„	„	„	„	„	„
	231	„	<i>oweni</i>	„	„	„	„	„	„
	232	„	„	„	„	„	„	„	„
	233	E	„	„	„	„	„	„	„
	234	F	„	„	„	„	„	„	„
17	235	G	„	„	„	„	„	„	„
	236	„	<i>australis</i>	„	„	„	„	„	„
	237	H	<i>oweni</i>	„	„	„	„	„	„
	238	„	<i>bulleri</i>	„	„	„	„	„	„
	239	I	<i>australis</i>	„	„	„	„	„	„
	240	K	„	„	„	„	„	„	„

## H. THE FORE-LIMB.

## References.

<i>Cl</i>	Alar claw	<i>Phal. 2', 2'', and 2'''</i>	The phalanges of the second digit
<i>Op.</i>	Carpale.	<i>Phal 3.</i>	Phalanx of third digit.
<i>Op Metp.</i>	Carpo-metacarpus	<i>Ra</i>	Radius.
<i>dist</i>	Distale.	<i>ra.</i>	Radiale.
<i>dist 1-3.</i>	The separate distalia of early stages.	<i>ra dist.</i>	Radio-distale
<i>Hu.</i>	Humerus	<i>Ul.</i>	Ulna.
<i>Metp 1-3</i>	The three metacarpals.	<i>ul.</i>	Ulnare.

Plate	Fig	Stage	Species	
17	241	Adult	<i>australis</i>	Left manus, dorsal aspect
	242	"	<i>oweni</i>	" " " "
	243	"	"	" " " "
	244	"	"	" " " "
	245	"	<i>bulleri</i>	" " " "
	246	"	"	" " " "
	247	"	"	" " " "
	248	"	"	Right " " "
	249	"	"	Left " " "
	250	"	<i>haastii</i>	" " A dorsal, B palmar aspect
	251	"	"	" " dorsal aspect
	252	"	"	Right " " "
	253	"	<i>marina</i> = <i>bulleri</i>	Left " " "
	254	E	<i>oweni</i>	Horizontal section of left fore-limb (combined figure)
	255	"	"	" " " " " " single section, further dorsal than the preceding
	256	F	"	" " " " manus (combined figure)
	257	G	<i>australis</i>	Left manus, dorsal aspect, restored from sections
	258 } 259 }	"	"	Single horizontal sections of left manus
	260	"	<i>oweni</i>	Horizontal section of left manus
	261	H	"	" " " " " " } combined figures
	262	"	<i>bulleri</i>	" " " " " " }
	263	I	"	" " " " " " }
	264	"	<i>australis</i>	" " " " " " }
18	265	K	"	Left fore-limb, dorsal (outer) aspect
	266	"	"	Horizontal section of left carpo-metacarpus
	267	"	<i>bulleri</i>	Left manus, dorsal aspect
	268	"	"	Horizontal section of left carpo-metacarpus
	269	L	<i>australis</i>	Left manus, dorsal aspect
	270	"	"	Horizontal section of left carpo-metacarpus
	271	"	<i>oweni</i>	Left manus, dorsal aspect
	272	M	<i>australis</i>	" " " "
	273	"	<i>oweni</i>	" " " "

I THE PELVIS.

References

<i>actb</i>	Acetabulum	<i>Pr. Il</i>	Pre-ilium
<i>Ant trch</i>	Antitrochanter	<i>Pt Il</i>	Post-ilium
<i>Isch</i>	Ischium	<i>Pu</i>	Pubis
<i>Pect pr</i>	Pectineal process		

Plate	Fig	Stage	Species	
18	274	D	<i>oweni</i>	Left innominate, external aspect, restored from sections
	275	E	"	" " " " " "
	276	F	"	" " " " " "
	277	G	"	" " " " " "
	278	L	<i>australis</i>	" " " " " "
	279	O	"	" " " " " "

K. THE HIND-LIMB

References.

<i>asc pr</i>	Ascending process of tibiale	<i>Fib</i>	Fibula
<i>cent 1</i>	Preaxial centrale.	<i>fib</i>	Fibulare
<i>cent 2.</i>	Postaxial "	<i>Mt tsl 1-5</i>	Metatarsals
<i>dist.</i>	Distale	<i>Tib</i>	Tibia
<i>Fe</i>	Femur	<i>tib</i>	Tibiale.

Plate	Fig	Stage	Species	
18	280	D	<i>oweni</i>	Left leg, dorsal aspect, reconstructed from sections
	281 }	"	"	Single horizontal sections of tarsus
	282 }	"	"	"
	283	E	"	Left leg, dorsal aspect, reconstructed from sections
	284	"	"	Horizontal section of tarsus
	285	F	"	Right pes, dorsal aspect, reconstructed from sections
	286	"	"	Horizontal section of tarsus
	287	"	"	Vertical " "
	288	"	"	Horizontal " "
	289	G	"	Left leg, dorsal aspect
	290	"	<i>australis</i>	Horizontal section of tarsus
	291	"	"	" " "
	292	Adult	<i>haastii</i> ?	Posterior (plantar) aspect of mesotarsal joint

## L MUSCLES OF THE WING

*References*

<i>ancon</i>	M anconeus	<i>flex prof int</i>	M flexor profundus internus gallina- ceorum
<i>biceps</i>	M biceps brachii	<i>Hu</i>	Humerus
<i>brach ant</i>	M brachialis anticus	<i>interos dors</i>	M interosseus dorsalis
<i>brach int access</i>	M brachialis anticus accessorius	<i>pect maj</i>	M pectoralis major
<i>Cor brach sup</i>	M coraco-brachialis superior	<i>pron</i>	M pronator
<i>Cor brach inf</i>	M coraco-brachialis inferior	<i>Ra</i>	Radius
<i>Up Metap</i>	Carpo-metacarpus	<i>Subcl</i>	M subclavius
<i>ext carp ul</i>	M extensor carpi ulnaris	<i>supin</i>	M supinator,
<i>ext ind prop</i>	M extensor indicis proprius	<i>teres</i>	M teres
<i>ext metacarp rad brev</i>	M extensor metacarpi radiatis brevis	<i>triceps</i>	M triceps brachii
<i>flex carp rad</i>	M flexor carpi radialis	<i>Ul</i>	Ulna
<i>flex dig prof</i>	M flexor digitorum profundus		

Plate	Fig	Stage	Species	
19	293	Adult	<i>australis</i>	Muscles of the shoulder and wing, dorsal (external) aspect
	294	"	"	" fore-arm and hand, palmar aspect
	295	"	<i>bulleri</i>	" " " dorsal "
	296	"	"	" " " palmar "

## M. THE BRAIN AND EYE

*References*

<i>ant com</i>	Anterior commissure	<i>opt chs</i>	Optic chiasma
<i>ch plv</i>	Choroid plexus	<i>opt cœ</i>	Optocœle (optic ventricle)
<i>corp call</i>	Corpus callosum	<i>opt com</i>	Optic commissure
<i>corp stri</i>	Corpus striatum	<i>Opten</i>	Optencephal (optic lobe)
<i>Bs.opt</i>	Basiopticus	<i>Opt thal</i>	Optic thalamus
<i>di cœ</i>	Diacœle (third ventricle)	<i>Opt ves</i>	Optic vesicle
<i>Dien</i>	Diencephal	<i>Pect</i>	Pecten
<i>ep cœ</i>	Epicœle (cerebellar ventricle)	<i>ped crb</i>	Peduncle of cerebrum
<i>Epen</i>	Epencephal (cerebellum)	<i>ped cbl</i>	" cerebellum
<i>floc</i>	Flocculus	<i>Pin</i>	Pineal body
<i>for M</i>	Foramen of MONRO	<i>post com</i>	Posterior commissure
<i>inf</i>	Infundibulum	<i>Pros en</i>	Prosencephal (cerebral hemisphere)
<i>lam term</i>	Lamina terminalis	<i>Pi Pin Dvertic</i>	Prepineal diverticulum
<i>Mesen</i>	Mesencephal	<i>pros cœ</i>	Prosocœle (lateral ventricle)
<i>Met en</i>	Metencephal (medulla oblongata)	<i>Pty</i>	Pituitary body
<i>Ms cœ. &amp; iter</i>	Mesocœle	<i>Rhinen</i>	Rhinencephal (olfactory lobe)
<i>mt cœ.</i>	Metacœle (fourth ventricle)	<i>vel int</i>	Velum interpositum
<i>Nr II-XII</i>	Cerebral nerves	<i>Valv Viens</i>	Valve of VIEUSSENS

Plate	Fig	Stage	Species	
19	297	Adult	<i>bulleri</i>	Entire brain, dorsal aspect
	298	"	"	" ventral "
	299	"	"	" left side
	300	"	"	Brain with hemispheres and cerebellum removed and right opto-coele exposed
	301	"	<i>australis</i>	Sagittal section of brain
	302	I	"	Transverse section through diencephal
	303	"	"	" " " mesencephal
	304	E	<i>oweni</i>	Brain from above prosa-, dia-, and opto-coele exposed on left side
	305	"	"	Entire brain from left side
	306	F	"	Brain from above diacoele exposed on left side
	307	"	"	Sagittal section of brain
	308	G	<i>australis</i>	Entire brain, dorsal aspect
	309	"	"	" " left side
	310	H	<i>oweni</i>	" " ventral aspect
	311	I	<i>australis</i>	Portion of retina with pecten

} reconstructed from sections

III *On the Course of the Fibres of the Cingulum and the Posterior Parts of the Corpus Callosum and Fornix in the Marmoset Monkey.*

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[ PLATES 20—24 ]

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THE present investigation has for its scope to follow out the course of certain fibres in the brain which have hitherto escaped minute investigation.

*Introduction.*

There are various methods which have been adopted to work out the course of the fibres in the brain The method by dissection of the brain with the scalpel has been

much employed, and though it is doubtless of value in tracing out the coarser strands, it is open to the objection that the parts are very much displaced by the operation necessary to follow out the fibres, and also that relations may be artificially produced which do not actually exist. Moreover it is quite impossible to trace the fibres to their ultimate ending, as this can only be accomplished by the use of the microscope.

The methods of tracing the fibres by producing degeneration in the different tracts by dividing them during life, and also the method of examining the period in foetal life at which the fibres acquire their medullated sheath, which has been employed by FLECHSIG, give most certain results, but they present great difficulties when a large system of fibres like the cingulum, which courses round the whole extent of the brain, has to be minutely examined.

It was also found that to work out the course of the cingulum it was quite impossible to perform this satisfactorily in a brain like that of Man or the Monkey, which possessed a deep calloso-marginal sulcus, round which it was probable that the fibres of the cingulum would have to pass on their way to other parts, and which would prevent them from being traced in any other plane than that of the frontal. Owing to the unwieldy size of the human brain it is very difficult, if not impossible, to trace the fibres under the microscope, and pathological anatomy has not hitherto thrown any light on the course of the fibres treated of in this paper.

It was therefore thought desirable to follow out these fibres by making serial sections in different planes of a small but high brain like that of the Marmoset, and by using reagents which especially differentiate the medullated fibres.

The part of the brain which has been investigated in the present research comprises the cingulum or the longitudinal fibres of the gyrus fornicatus, the body and the posterior pillars of the fornix, and the connections of the posterior part of the body and the splenium of the corpus callosum with the occipital and temporo-sphenoidal lobes.

Before proceeding to a description of the work I shall cite references from some of the best-known text-books, and for this purpose I shall give extracts from QUAIN'S 'Anatomy,' 9th edition, from works on the Brain by MEYNERT, SCHWALBE, OBERSTEINER, WERNICKE, HUGUENIN, HENLE, and from FOVILLE'S 'Atlas of the Brain.' These descriptions apply to the brain of Man only, but, as far as I can ascertain, there is no account published of the minute anatomy of the Marmoset's brain. For the sake of convenience each of the above-named structures will be described separately as it appears in the three different planes, and after tracing it through these different directions a *résumé* will be given of the connections and appearances of each structure as a whole, *i.e.*, in the three dimensions of space. To prevent confusion the references to the various authors for each of the different parts under consideration will be put separately with the description of each part.



*Method of Investigation*

The parts of the brain under examination are contained in the interior of the cerebrum and are approached with great difficulty for the purposes of producing degeneration during life, while, as far as we know at present, pathological changes in Man do not throw much light on the subject

It has seemed to me that the best results would be obtained by making serial sections in different planes of the brain of one of the lower animals, which should be small enough for easy manipulation, and yet at the same time should be sufficiently high in the animal scale for comparison with the brain of Man. For this reason the brain of the Marmoset was almost entirely used, and I have to thank Mr F. BEDDARD, prosector to the Zoological Society, for kindly providing me with material. The different species of Marmoset used comprise the *Hapale jactans* and *Hapale penicillata*.

In one case the brain of the Bonnet Monkey, *Macacus sinicus*, was employed

*Details of Method* --The brains of the Marmoset were put direct into a 3 per cent. solution of bichromate of potassium, where they were hardened in the usual way from two to four months and in one case for twelve months. After hardening, the brain was embedded in celloidin and cut into sections by SCHANZE'S microtome, from a 50th to a 25th of a millimetre thick. The sections were stained by WEIGERT'S hæmatoxylin method,\* and in other cases by PAL'S† modification of WEIGERT'S method. The sections were dehydrated in the ordinary way by absolute alcohol, clarified by oil of cloves or organon oil, and mounted in Canada balsam. The organon oil, the use of which was introduced by WEIGERT, has the advantage over oil of cloves in that it does not dissolve out the celloidin, which is thus able to hold together the finer parts of the section and prevent its being torn to pieces in the process of clarifying. It was found, however, that after the use of organon oil, owing probably to the contraction exerted by the celloidin, these large sections after the application of the cover glass did not present a perfectly flat field when viewed with the higher powers of the microscope, and it was difficult to trace fibres in sections treated in this way.

To obviate this difficulty, and at the same time to prevent the sections from being damaged, the following plan was adopted in some of the sections: they were dehydrated on the slide by absolute alcohol, this was run off without disturbing the sections, which were then clarified by adding organon oil. When this was completed, the oil was drained off the slide as much as possible, and oil of cloves was carefully added. This was again run off after dissolving the celloidin, drained, and the preparation mounted in Canada balsam dissolved in xylol.

Some of the sections were also cut after imbedding in paraffin. The brain was

\* 'Fortschritte der Medicin,' 1884, p 190, 1885, No 8

† 'Brit Med Journal,' 1888, vol 1, p. 510

hardened in methylated alcohol, it was then put into a 3 per cent solution of bichromate of potash for two weeks, washed in water and in methylated alcohol and put direct into WEIGERT'S hæmatoxylin for three or four days, developed in the usual way, imbedded in paraffin after passing through absolute alcohol and oil of cloves, and the sections mounted after removing the paraffin by xylol.

*Direction of the Sections*—In the following descriptions the sections of the brain were cut in the following planes, viz, sagittal, horizontal, frontal, and fronto-oblique. The sagittal sections were made in a plane which is in a vertical and an antero-posterior direction, in fact parallel to the median surface of one hemisphere. The horizontal sections were cut in a plane which would be horizontal in Man or Monkey when in the erect position. This plane is, therefore, at right angles to the sagittal and along the greatest length of the brain, namely, from the tip of the frontal lobe in front to the tip of the occipital behind. The frontal sections were cut in a plane at right angles to the horizontal, viz, transversely across both hemispheres and in a vertical line. In the fronto-oblique sections the plane was transverse, but instead of being vertical or horizontal it inclines upwards and forwards and downwards and backwards so as to be parallel to the long axis of the medulla oblongata and pons Varolii.

In this way sections were obtained of the brain corresponding to the three dimensions of space; and, for the sake of comparison with the brain of Man, the animal is considered to be in the erect posture with the face directed forwards, and not in the position of walking on four legs, when the face would be directed towards the ground.

In preparing the series for every one plane, all the sections were examined as they were cut, but only those were mounted which presented a slight difference from the section preceding it.

We thus have in the sagittal plane a complete series beginning at the middle line and extending outwards as far as the external capsule; in the horizontal direction a complete series from the upper surface of the centrum ovale above to the level of the crus cerebri below, while in the frontal and fronto-oblique planes the series extends from the level of a fronto-oblique plane drawn through the anterior part of the crura cerebri, and extending backwards to a similar plane through the occipital lobe and at a point a short distance behind the most posterior limit of the lateral ventricle.

In this way it was considered that the different tracts of fibres might be traced from section to section in the individual series, and that points of difficulty which could not be ascertained in one section could be elucidated by examining the part in the other planes, and by combining the appearances seen in the three planes, a mental image of the structure in the three dimensions of space could be obtained.

*Description of the Brain of the Marmoset (Hapale penicillata).*

The brain of the Marmoset measures in its greatest length from the tip of the frontal lobe in front to the tip of the occipital behind from 3.2 to 3.5 centimetres, and across its broadest part, viz., across the temporo-sphenoidal lobes 2.5 to 2.7 centimetres. Its greatest depth from the vertex to the inferior surface of the temporo-sphenoidal lobe is about 2.2 centimetres.

The frontal and occipital lobes are well developed, and the latter completely overlap the cerebellum. The most striking part about the Marmoset's brain is the almost complete absence of convolutions, the surface being quite smooth and possessing only a few of the chief fissures. Of these only the following can be made out, on the outer surface the *fissure of Sylvius* is well marked (Plates 23, 24, figs 34, 39, *S F*\*), and has a straight direction upwards and backwards, reaching a point about the middle of the outer surface of the hemisphere. The fissure is represented only by its horizontal limb, as no trace of its anterior ascending limb can be found.

In the temporo-sphenoidal lobe there is a distinct indentation below and parallel to the fissure of Sylvius. This represents the *parallel sulcus* in the brain of other animals.

There is no definite depression for the *fissure of Rolando*, unless its position is indicated by a blood-vessel which runs in the direction corresponding to this fissure in other animals.

On the median aspect of the Marmoset's brain, the surface is very smooth, and there is only the slightest indication of a *calloso-marginal sulcus*, but on frontal section especially in the anterior part it can be seen as a very slight superficial depression in the cortical grey matter.

The most marked fissure on the median surface is the *calcarine* (figs 5, 34, 44, *F C*.) It commences behind, near the tip of the occipital lobe and runs forward, at first horizontally, and then turns downwards and forwards. It appears anteriorly to join the dentate or hippocampal sulcus in sagittal sections (see fig 10, *H S*, *F C*). But this is really not the case, as on following these sagittal sections outwards, the isthmus of the gyrus fornicatus is seen to separate the two, there is no doubt, however, that the calcarine fissure at its commencement forwards takes origin very near to the dentate (*cf* fig 43 right, *H S*, *C.S*). The calcarine is therefore a fissure of very great importance.

In fronto-oblique sections (fig 44) the direction of this fissure is seen to be in a direction outwards and downwards from the median line, and, as will subsequently be seen, it is in the cortex bounding this sulcus that we have the system of fibres which I have termed the calcarine.

The *Dentate* or *Hippocampal* sulcus (figs 10, 35, 43 right, *H S*) extends from the under surface of the gyrus fornicatus above, downwards along the anterior edge of the

\* See Explanation of Plates, pp 197-199

gyrus hippocampi to the hollow in the hook of the uncinate or hippocampal convolution below. It is seen very well in sagittal sections, where it is bounded by the fascia dentata. In frontal sections it forms a deep groove on the median aspect of the temporo-sphenoidal lobe (fig 40, *H.S*), and in horizontal sections it is particularly well marked, separating the fascia dentata from the gyrus hippocampi.

In the above description the dentate sulcus has been traced to the under surface of the gyrus fornicatus above. In frontal sections, however, this sulcus can be seen to exist on the inferior surface of the gyrus fornicatus, and lying on the corpus callosum as far forward at least as the vertical level of the optic commissure, as has already been described in other animals \*

It will therefore be seen that with the exception of the gyrus hippocampi with its fascia dentata, and the grey matter bounding the deep calcarine fissure, the brain of the Marmoset has no convolutions. This property is of the highest importance in working out the fibres of the cingulum. Owing to the absence of a calloso-marginal sulcus along the median face of the hemisphere the gyrus fornicatus and its contained cingulum is not separated off from the rest of the median surface (*i.e.*, the gyrus marginalis) and the centrum semi-ovale, as it is in the brain of Man or the Macaque Monkey, but this sulcus in the Marmoset is represented by a slight indentation along the median line, and by the inner surface of the centrum semi-ovale presenting in frontal sections (figs. 39, 40) a slight concavity, at the lower end of which is situated the cingulum in close contact with the corpus callosum and the centrum semi-ovale.

The fibres of the cingulum will not, therefore, have to wind round the deep calloso-marginal sulcus, as in Man and the Macaque Monkey, but can pass direct into the centrum semi-ovale, and their course will thus be brought into view in one of the three planes of sections, a result which it would be impossible to obtain in the two other brains referred to above.

I will now proceed to a detailed description of the structures under consideration, and will begin with the cingulum, giving first the views of the different authorities on the subject.

### *Cingulum.*

Called also fibres of the gyrus fornicatus, fillet of the corpus callosum (MAYO).

*Previous Descriptions.*—These fibres are described by QUAIN† “as constituting the white substance of the gyrus fornicatus, and they take a longitudinal course immediately above the transverse fibres of the corpus callosum.

“In front they bend downwards within the gyrus to which they belong, and are connected with the anterior perforated space, being joined by certain longitudinal fibres which run along the under surface of the corpus callosum near the middle line. Behind they turn round the back of the corpus callosum, and thence descend to the

\* Cf ZUCKERKANDL, ‘Ueber das Riech-Centrum.’

† QUAIN’S ‘Anatomy,’ 9th edition, p. 356.

point of the temporo-sphenoidal lobe, where, according to FOVILLE, they again reach the perforated space. Offsets from these fibres pass upwards and backwards into the secondary convolutions derived from the gyrus fornicatus in the longitudinal fissure.

According to SCHWALBE\* “Along the whole course of the gyrus fornicatus, there is a longitudinal system of fibres, situated on the mesial surface of the hemisphere, starting from the lamina perforata anterior it is situated near to the genu, the body and the splenium of the corpus callosum, it then follows the course of the gyrus hippocampi to its ending in the gyrus uncinatus. The greater part of these fibres is covered by the grey cortex inside the gyrus fornicatus and gives off fibres to neighbouring convolutions and receives fresh ones in return, it becomes smaller in the isthmus of the gyrus fornicatus, and again enlarges in the gyrus hippocampi, in the central medulla of which it ends. A small component part of this system of fibres, which remains attached to the upper surface of the body of the corpus callosum, after the gyrus cinguli has become detached from it, is known as the ‘tænia tecti’. This set of fibres does not pass into the medullary centre of the gyrus hippocampi, but turns behind the splenium corporis callosi on to the surface of the gyrus hippocampi, forming the peculiar peripheral medullated layer, described as *substantia reticularis*, which again forms the superficial medullary lamina (Kernblatt) between the subiculum cornu Ammonis and the fascia dentata.”

The cingulum, as described by MEYNERT,† “surrounds the corpus callosum, above it lies a broad convolution after removing the sulcus calloso-marginalis. The medulla of this convolution is joined continuously on to the cingulum as well as the larger and shorter fasciculi proprii of the gyrus fornicatus which cover the cingulum, and it is also joined to the first frontal and parietal convolutions surrounding this gyrus. The lowest bundle of the cingulum lying next to the corpus callosum (*nervus Lancisi*) connects the Ammon’s horn (*substantia reticularis*) with the olfactory convolution. After the cingulum has formed a covering for the calloso-marginal sulcus, and has formed all these connections with the cortex, its bundles continue backwards below the splenium corporis callosi, and at the highest point join the fasciculi proprii upon which are laid the calcarine and fronto-occipital sulci, these connect the cingulum with the gyrus lingualis.”

MEYNERT‡ states that, according to ARNOLD, the bundles run through the corpus callosum from the cortex of the gyrus fornicatus to join the fornix and also into the septum pellucidum, therefore other convolutions besides the gyrus uncinatus send “projection-bundles” through the fornix.

HUGUENIN§ describes the cingulum in terms similar to that of QUAIN, and other authors, and states that “it ends posteriorly and inferiorly in the region of the nucleus

\* SCHWALBE, ‘Lehrbuch der Neurologie,’ Erlangen, 1881, p. 759

† ‘Psychiatrie,’ Wien, 1884, p. 37

‡ *Op cit*, p. 39

§ ‘Anatomie des Centres Nerveux,’ 1879, p. 126.

amygdalæ, with which it has connections which have not yet been clearly elucidated. Behind the splenium of the corpus callosum the bundle is thinner, and again increases in thickness as it descends in the hippocampus, this difference in size is due to the fact that different systems of fibres contribute to its formation. There is no doubt that there are fibres here which connect the internal surface of the frontal convolutions with the cortex of more distant parts, viz, the apex of the temporal lobe. During the course of this bundle, it forms various intermediate stations of communication, and this is proved by the fact that the bundle of fibres, when traced from their beginning to their ending, do not get progressively smaller, but below the corpus callosum they become larger, as also in the temporal lobe. In the course of the cingulum above the corpus callosum, numerous other fibres from the neighbouring parts of the cortex, join it and then leave it again after a longer or shorter course; this small system of arciform fibres is united to the fibres which go the whole length of the cingulum, these fibræ arciformæ resemble the fibræ propriæ of other parts, and help to swell the size of the cingulum above the corpus callosum; they are least numerous behind the splenium corpus callosi. . . . In Mammalia the cingulum receives at its anterior part fibres from the medulla of the olfactory lobe. . . . These longitudinal fibres of the cingulum are crossed by transverse fibres from the medullary centre of the hemispheres; these terminate in the cortex of the gyrus fornicatus, and are the fibres of the corpus callosum. It is not known whether any fibres of the corona radiata also follow this direction. On the other hand the fibres of the cingulum itself are distributed to the cortex of all the parts situated above it. . . . We have called the bundle of fibres lying beneath the gyrus fornicatus (circonvolution de l'ourlet) a system of association fibres . . . And as the different parts which they unite have such marked physiological differences we are quite justified in considering these fibres as systems connecting the various functional regions of the brain."

HUGUENIN\* also states that "the medulla of the olfactory lobe is united through its internal root to the medulla of the gyrus fornicatus (anterior part), while, by the external root, the olfactory nerve is joined to the medulla of the gyrus hippocampi and to the subiculum of the cornu Ammonis, that is the system of association fibres lying under the gyrus fornicatus"

In FOVILLE'S 'Atlas,'† Plate 14, fig 1, and on Plate 18, fig. 1, the inner surface of the human brain is dissected to show fibres coursing upwards and backwards from the horizontal part of the cingulum along the connecting gyri to the marginal convolution, also to the convolutions below the calcarine fissure, and to the gyrus hippocampi and the nucleus amygdalæ. These are the fibres described above by HUGUENIN, and they evidently take their course on the surface of the convolution, forming a system of "fibræ propriæ," and do not penetrate into the mass of fibres of the centrum ovale

\* *Loc cit*, p. 131

† Paris, 1844.



According to OBERSTEINER,\* the cingulum is described "as an arched system of fibres which course in the medullated substance of the gyrus cinguli. The cingulum lies through the greater part of its course on the corpus callosum at that point where its fibres begin to radiate into the centrum ovale, and, as a rule, the cingulum can be seen even in the lower animals, in frontal sections through the hemisphere, as a round bundle of transversely cut fibres"

"We see, therefore,† that in the striæ longitudinales mediales (nervus Lancisi), including the fascia dentata (the outer zone of fibres), we have to look for the real edge of the superficial fibres of the cortex.

"Anteriorly, the striæ longitudinales mediales are continued into the peduncles of the corpus callosum, which descend to the base of the brain, posteriorly, they enter the fascia dentata of the cornu Ammonis, as well as the layer of white matter called the substantia reticularis Arnoldi.

"In some respects, viz., the arrangement of the third\* layer, the cortex of the subiculum cornu Ammonis has an unmistakable resemblance to that of the gyrus cinguli"

*Sagittal sections.*—To understand the direction and disposition of the fibres of the cingulum, it will be best to describe it first in sagittal sections, beginning at the median line and passing outwards. Further, it will be convenient to divide it up into three parts, viz., a horizontal, situated in the gyrus fornicatus above the corpus callosum; an anterior part extending in the gyrus fornicatus from the front of the genu of the corpus callosum down to the anterior perforated spot; and a posterior part contained in the isthmus of the gyrus fornicatus and hippocampal gyrus and reaching from behind the splenium of the corpus callosum along the temporo-sphenoidal lobe to its anterior end.

In the sagittal direction after cutting through the grey cortex corresponding to the marginal convolution and the gyrus fornicatus in man, we reach the fibres of the cingulum, which appear first as a faint line of horizontal fibres, running from behind forwards and coursing round the front of the corpus callosum. They lie just above the corpus callosum and are distinct from the fibres of the centrum semi-ovale, except at the most anterior part, where the two seem to blend together.

In front of the genu of the corpus callosum, the anterior fibres have a direction downwards and backwards. They seem to arise in the centrum ovale and run downwards, but where they end cannot be accurately ascertained. At the most inferior part, i.e., next to the anterior perforated spot, the lowest fibres seem to be continued into the olfactory nerve and especially its internal root. It would thus appear that the olfactory nerve is connected with fibres of the cingulum, which proceed from the centrum ovale of the extreme anterior frontal region, and not with those which come from that part of the cingulum which is above the corpus callosum, i.e., the horizontal part.

\* 'Nervosen Centralorgane,' 1888, p. 347.

† *Loc. cit.*, p. 359



It may be remarked here that this root of the olfactory nerve also arises from a group of cells in the angle formed by the nerve with the anterior descending part of the cingulum

In the next sections the horizontal part of the cingulum, *i.e.*, the part above the corpus callosum, comes into view and it can be divided into two parts, an anterior and a posterior. The anterior part lies directly in contact with the upper surface of the corpus callosum, whereas the posterior part is separated from the corpus callosum by the grey matter of the gyrus fornicatus. This difference in appearance can be explained by examining frontal sections, where it is seen that in sections at the vertical level of the optic commissure (see fig. 39, *Cing. h*), the principal axis of the cross section of the cingulum is almost vertical, whereas in sections through the more posterior part of the corpus callosum (fig. 40, *Cing. h.*) this axis is horizontal, or in other words, the breadth of the cortex corresponds to the gyrus fornicatus, increases in a horizontal transverse direction as we pass backwards, and in so doing it makes the cross section of the cingulum become more horizontal. It follows from this that a sagittal section of the Marmoset's brain would, at the vertical level of the optic commissure, cut through the cingulum lying on the corpus callosum without passing through any grey matter, while more posteriorly more of the grey matter would appear between the cingulum and the corpus callosum (see p. 154).

The anterior part of the horizontal cingulum lies, as we have seen, on the corpus callosum, and has a direction forwards and downwards, parallel to the upper surface of the corpus callosum. The connexions of its fibres are very difficult to ascertain; posteriorly they seem to come from the cortex of the gyrus fornicatus, and anteriorly they appear to end in the centrum ovale, but this is not at all certain. In the posterior part of the horizontal cingulum the connections are more decided. Here, as has already been mentioned, the fibres of the cingulum are separated from the corpus callosum by the intervening cortex of the gyrus fornicatus (figs. 1-4).

As this posterior part of the horizontal cingulum comes more in view as we proceed outwards, the anterior part which was seen to be close on to the corpus callosum gradually disappears, till in fig 1 we have only the posterior part visible. This would show that the horizontal part of the cingulum is not parallel to the median line, but that its direction runs backwards and outwards, and, therefore, it is not possible to see its whole extent in any one section cut parallel to the median surface. In figs 1-4, the posterior part of the cingulum forms an arch beneath the centrum semi-ovale, and contains in its concavity the cortex of the gyrus fornicatus. The arch consists of fibres having an antero-posterior direction; its posterior end appears to spring from that part of the gyrus fornicatus which is posterior to the corpus callosum, *i.e.*, the commencement of the isthmus, and the anterior leaves off abruptly near the upper surface of the corpus callosum. On microscopical examination a very definite arrangement of its fibres can be made out, posteriorly the arch receives fibres from the cortex of the gyrus fornicatus, and then along the whole convexity of the arch the

fibres which it received posteriorly run forward and are then directed upwards and forwards into the centrum ovale. The arch is therefore not formed by a continuity of fibres from end to end, but each fibre runs for a certain length in it, and then turns upwards into the centrum ovale. Whether the cavity of the arch receives any fresh fibres from the gyrus fornicatus it is not possible to say for certain, but it is certain that fibres do come from the isthmus behind the corpus callosum. We have here, therefore, a relay of fibres whose direction is always from behind forwards and upwards to pass into the centrum semi-ovale.

The fibres which are most inferior in the arch, *i.e.*, those nearest to the corpus callosum, start their upward course into the centrum semi-ovale at a more anterior point than the fibres which form the superior convex part of the arch, or, in other words, the more anterior fibres are nearer to the median line, and also pass up into the centrum ovale anteriorly to the more external fibres.

The fibres which pass into the centrum ovale run upwards and forwards, and although they can be traced half way through its vertical depth, it has been impossible, owing to their complex arrangement, to trace them to the cortex on the vertex of the brain. It is suggested, however, that probably such is their destination.

As we pass to sections which are further removed from the middle line, the arch of the cingulum becomes smaller at the expense of its anterior part (fig 4), and the gyrus fornicatus diminishes also in size until we reach the point where the cingulum is cut through by the fibres coming out from the posterior part of the corpus callosum to sweep round into the occipital lobes forming what is known as the tapetum.

The posterior fibres of the arch of the cingulum, *i.e.*, behind the corpus callosum, which are situated in the hinder part of the gyrus fornicatus, here end in the form of a bulb (fig 5 *Cing p*), whence fibres pass down to the superficial surface of this convolution (fig 5, *Sf*).

The part of the cingulum in front of the intercepting fibres of the corpus callosum soon disappears in the next sections, leaving only the bulbous portion behind the splenium of the corpus callosum (fig. 5).

This bulbous enlargement comes into close relationship with a system of fibres which we may call the calcarine fibres (fig 5, *Cf*) (by this is meant the fibres contained in the convolution which, in the Marmoset, surrounds the prolongation of the calcarine fissure within the occipital lobe, see p. 162), and it forms the central white matter of the portion of the gyrus fornicatus which remains posterior to the corpus callosum, lying intermediately between the horizontal and posterior divisions of the cingulum.

The fibres in this bulbous formation of the cingulum soon assume an oblique direction, and appear in these sections as points, or in short lengths, where they are cut directly across or obliquely, and this direction of the fibres persists for some

distance, as the same appearance is seen in as many as six or seven successive microscopical sections of this series (figs. 5-9).

During this course the direction of the fibres is in a plane at right angles to the sections, and they form part of the inner wall of the posterior cornu of the lateral ventricle, being separated by the ventricle from the posterior part of the corpus callosum and its tapetum.

The posterior part of the gyrus fornicatus soon begins to be prolonged downwards and forwards (fig. 9) to join the hippocampal or uncinata convolution, forming what is known as the isthmus of the gyrus fornicatus. The relation of the isthmus of the gyrus fornicatus to the calcarine fissure has been referred to in the anatomical description of the Marmoset's brain (p. 139).

The bulb of the cingulum, whose fibres, as we have seen above, have assumed a transverse oblique direction, now send a prolongation of fibres downwards and forwards along the isthmus of the gyrus fornicatus (fig. 10, *Cing. p.*), while at the same time the superficial fibres of the gyrus hippocampi (*Sf.*) are prolonged along the dentate sulcus (*H.S.*). The former fibres are soon seen (fig. 11, *Cing. p.*) to sweep downwards and forwards in a thick leash in front of the fibres of the corona radiata which are continuous with those of the occipital region below the calcarine sulcus, into the descending hippocampal gyrus.

The cingulum then courses along the centre of the hippocampal gyrus to end in the cortical surface on the inferior part of the temporo-sphenoidal lobe, but it has no connection with the nucleus amygdalæ situated in front of the uncinata or hippocampal convolution.

We thus have the third or posterior part of the cingulum in its entire extent reaching from behind the forceps major above, down to the anterior part of the temporo-sphenoidal lobe below. In this extent its size does not vary much, except that at the lower part it swells out before finally tapering off.

In sections still further removed from the middle line the fibres of the cingulum are intercepted in the isthmus of the gyrus fornicatus by another band of fibres. These come from that part of the corpus callosum which is known as the forceps major (fig. 11, *F.M.*), and which is situated between the main body of the corpus callosum above and the upper end of the cortex of the hippocampal or uncinata convolution below, and just anterior to the descending fibres of the cingulum, from which latter it can be distinguished by its oblique direction downwards and backwards, and by the fact that its fibres are stained a much deeper colour than the cingulum.

These fibres of the forceps major (fig. 12, *F.M.*) course downwards and slightly backwards through the outer fibres of the cingulum, which they cross at an oblique angle, and their dark stained fibres (with WEIGERT's method) are in marked contrast to the paler fibres of the cingulum. (See corpus callosum, p. 170.)

After this decussation of the two sets of fibres, the cingulum diminishes very much in size and only its lower end remains.

As far as can be ascertained, this posterior part of the cingulum in the temporo-sphenoidal lobe does not send any fibres forwards into the uncinate or hippocampal convolution, but, on the contrary, communications (figs 11 and 12, *Sf*) from the superficial fibres of the cornu Ammonis run forwards and downwards to join the descending fibres of the cingulum. At its most inferior part it forms a thick leash of fibres (figs 11, 12, *Cing p*) situated just below the uncus of the uncinate convolution, and from this leash fibres are given off into the cortex on the inferior surface of the temporo-sphenoidal lobe, extending to its anterior end.

As far as can be judged from these sections the descending fibres of the cingulum do not end either in the hippocampal convolution or in the nucleus amygdalæ of the hippocampal lobule.

The direction of the individual fibres of this posterior portion of the cingulum in the upper part of its course is in the long axis of the tract, but at its lower end it receives offsets from the superficial fibres of the cornu Ammonis which enter it in a direction downwards and forwards. Here the tract of the cingulum is made up of a series of oblique fibres which spring from the superficial fibres just mentioned (figs 11 and 12, *Sf*), and go obliquely through the long axis of the cingulum to end in the cortex on the under surface of the temporo-sphenoidal lobe.

In sections nearer the middle line this most inferior part of the cingulum is crossed by the fibres of the alveus (see Fornix, p 184).

The appearance of the cingulum, as it is seen in horizontal sections will now be considered.

*Horizontal sections*—On making successive sections in a horizontal direction, beginning at the vertex and proceeding downwards, we arrive at the white matter of the centrum ovale (compare frontal sections of cingulum, fig 39) and soon the first indication of the cingulum (horizontal part) appears on the median side of the centrum ovale as fine fibres having a horizontal antero-posterior direction.

These fibres occupy about the second fourth of the whole length of the section. Posteriorly they end abruptly, but anteriorly and along their whole outer border they turn outwards into the centrum ovale, and it is observed that the fibres which are situated nearest to the middle line make this turn outwards into the centrum ovale at a point further forward than the fibres which are more external, similar to what was seen in sagittal sections.

On proceeding lower (fig. 13, *Cing h*), we find the cingulum as a band of horizontal fibres running in the antero-posterior direction. It presents two curves, namely, an anterior one which is convex towards the middle line and a posterior which is concave. This convexity explains how the anterior part of the cingulum is brought nearer to the median line in sagittal sections (see p 144) than the posterior part.

The cingulum is here bounded immediately on the inner side by the grey matter of the gyrus fornicatus (*GF.*), and on the outer side by the white matter of the centrum ovale (*CR*).

At this level its fibres turn outwards and forwards into the centrum ovale at its anterior end only, while posteriorly it forms a club-shaped bulbous enlargement, which comes into close contact with the calcarine fibres (*Cf*) (see p 145).

On tracing the fibres of the cingulum in succeeding horizontal sections (fig 14, *Cing. h*) the middle part disappears while the two ends continue, thus showing that the fibres have an arched direction from before back (comp sagittal sections, p 144).

In subsequent sections (fig 15) the only parts of the cingulum which are visible are these anterior and posterior ends of the arch

When we have passed the level of the inferior margin of the gyrus fornicatus and reached the fibres of the corpus callosum as they cross to the opposite hemisphere, the posterior end of the arch of the cingulum (fig. 16, *Cing. p*) appears in the gyrus fornicatus, close to and posterior to the hinder part of the corpus callosum, and in close apposition to the calcarine fibres (*Cf*) which bound it posteriorly. It presents a dotted appearance, showing that its fibres are cut across, and it is in marked contrast to the calcarine fibres, which have a more or less horizontal direction. The fibres of the cingulum are also distinguished from the calcarine by staining a slightly lighter colour. These two sets of fibres become very intimately connected, but lower down the calcarine are diminished in number. The cingulum while maintaining its descending direction appears to send off fibres which turn outwards and end abruptly at the inner wall of the lateral ventricle. They are in short lengths and are evidently the continuation of the cingulum in an oblique direction outwards and downwards (fig 18) These fibres lie close to the inner wall of the posterior cornu of the lateral ventricle, being only separated from that cavity by a thin layer of the corpus callosum, whose fibres have a direction at right angles to those prolonged from the cingulum. On the inner side of the cingulum are the calcarine fibres, which are distinct from those of the former. Consequently, at this level (fig. 22), we have on the inner wall of the posterior ventricular cornu (*L.v.p.*) the fibres arranged in the following order, beginning from the ventricle and going backwards and inwards.—

- 1st The fibres of the corpus callosum (*Spl.*).
- 2nd The prolongation from the cingulum, having a direction at right angles to the former (*Cing. p.*).
- 3rd The calcarine fibres, having a direction backwards, but less outwards than those of the cingulum (*Cf.*).

The 1st and 3rd of these fibres will be referred to later.

The fibres of the anterior part of the arch of the cingulum (figs. 16–22, *Cing. a*), are now seen in front of the genu of the corpus callosum in the anterior descending part of the gyrus fornicatus, where they send fibres forwards and outwards into the centrum ovale.

In tracing the posterior part of the cingulum arch downwards (fig 23, *Cing p*) its fibres are gradually pushed backwards and outwards by the formation of the hippocampus major (*CA*), which intervenes between the corpus callosum (*Spl*) and the cingulum, the latter thus comes to occupy the position of the fibres prolonged backwards from it above. The calcarine fibres, still lower (fig 28) form a faintly stained descending tract, showing only their cut ends (figs 28-34, *Cf*), and situated behind the commencing hippocampus major (*CA*). This tract of calcarine fibres is prolonged backwards from the neighbourhood of the cingulum along the inner wall of the posterior cornu and extends to the tip of the central white matter of the occipital region, its fibres presenting the appearance of points, *i.e.*, cut across (fig 34, *Cf*).

In all these sections (figs. 23-34) the cut-across cingulum lies behind the cornu Ammonis or hippocampus major (*CA*), and as we descend in the sections this becomes more developed, and at the same time the cingulum becomes flatter in appearance. It is in contact posteriorly with the tract of calcarine fibres (*Cf*) which are here continued along the inner wall of the posterior ventricular cornu, on the outer side of the cingulum is the forceps major (*FM*), from the splenium corporis callosi, which has now reached the posterior surface of the cornu Ammonis (fig. 29); its inner end projects into the cortex of the gyrus hippocampi, where it comes into contact with the superficial fibres of this gyrus (*Sf*, fig 29). In the above arrangement the forceps major is readily distinguished from the cingulum by the fact that its fibres are so much more deeply stained.

In fig 35 we have the superficial fibres (*Sf*) of the gyrus hippocampi very well marked, situated along the posterior edge of the dentate or hippocampal sulcus (*HS*) and with a horizontal direction, which later becomes descending. They lie just in front of the cingulum, arching round it, but no definite connection can be made out between them at this level.

The principal axis of the cingulum (as seen in these sections), which had been transverse, now assumes more of an antero-posterior direction, the external end becoming the more posterior (figs 34-38).

The calcarine fibres prolonged backwards along the inner wall of the posterior cornu have now (fig 35, *Cf*) a more horizontal direction, namely, outwards and backwards, and at right angles to the fibres of the forceps major, which is now (fig 37) beginning to pass backwards into the occipital region.

In figs 35 and 36 we have the calcarine fibres (*Cf*) forming the outer boundary of a strip of grey matter, which, if traced forwards to the free inner edge of the hippocampal gyrus, is found to contain there the vestige of a fissure which appears to arise out of the dentate or hippocampal sulcus (*HS*); this is the calcarine fissure (*FC*) which is seen fully formed in figs. 29-34, and consequently the strip of grey matter is the cortex forming the floor of the calcarine fissure (comp figs 41-45). This piece of cortex is bounded along the whole extent of its inner side by a layer of fibres (fig. 35, *Cf*) which have the same direction as the fibres on the outer side of



this cortex, *i.e.*, backwards and outwards, therefore these are the calcarine fibres of the inferior lip of the calcarine fissure. In the next section (fig 36) the two sets of fibres have begun to join, and later (fig 37) the cortex has disappeared and its place is taken by the calcarine fibres, having a direction backwards and outwards, while in fig 38 only the lowest part (*Cf.*) of these fibres is visible, the space being occupied by the forceps major.

From this it seems that these calcarine fibres can be traced round beneath the cortex at the bottom of the calcarine fissure, and that their direction is from the median line outwards and backwards, and after passing round the fissure they ascend vertically or obliquely along the inner surface of the posterior ventricular cornu in the cortex, forming the superior lip of the calcarine fissure (see p. 163), extending forwards to come into close relation with the cingulum.

Having now reached a level below the bottom of the calcarine fissure (fig 37) there is a great confusion of fibres, and those from the posterior part of the internal capsule and the optic radiations of GRATIOLET have begun to merge with the central white matter of the convolution which formed the inferior lip of the calcarine fissure, on the median aspect of the occipital lobe, fig 38, *C.R.*

In fact here the part of the occipital lobe on the outside of the calcarine fissure and of the lateral ventricle is merged with the part of the occipital lobe which is below that fissure.

The fibres of the cingulum still have the appearance of being cut across, and subsequently the most internal fibres of the hinder part of the internal capsule, which, in previous sections proceeded to the extreme posterior part of the occipital convolutions, now turn sharply round the lateral ventricle into the neighbourhood of the cingulum. This is owing to the fact that we have now reached a level near to the inferior surface of the occipital lobe, which, as we shall see further on, disappears altogether from the sections. At the same time the posterior cornu of the lateral ventricle gradually becomes shorter, receding from behind forwards, till at this level it does not extend farther back than the cingulum, in fact it almost ceases to exist as such.

In the next section the cingulum appears to consist of two parts, an external part associated with the system of fibres bounding the outer or ventricular surface of the cornu Ammonis and forming what is known as the alveus (see p. 188), and an inner set of fibres situated between the apex of the cingulum (as here seen) and the projection formed by the anterior border of the central medullary substance of the temporo-sphenoidal lobe. This latter is the part of the cingulum into which the fibres from the internal capsule (described above) seem to end. This division, though, perhaps, not very marked at this point, becomes more so further down.

In the next sections we get below the level of the occipital convolutions, and from this point downwards we have only to deal with the white matter of the descending temporo-sphenoidal lobe.



Here all the fibres from the internal capsule make a sharp curve inwards, almost at right angles to end in the temporo-sphenoidal lobe, and at the same time the conical projection of the cut across cingulum and the central medulla of this lobe have come together, the cingulum now merely forming a projection on the anterior part of the medullated substance.

The fibres of the cingulum here assume more of an oblique direction, and come in contact with fibres from the most internal part (*i.e.*, nearest to the ventricle) of the posterior fibres of the internal capsule. From the apex of the projection of the cingulum there is a large number of fibres passing between it and the superficial fibres of the cornu Ammonis (external medullated layer)

The cingulum now becomes less and less until it forms a small bulbar enlargement at the posterior end of the alveus, and the direction of its fibres is now distinctly forwards and inwards

As we proceed downwards the cingulum fibres become more separated by the descending cornu of the lateral ventricle from the mass of fibres forming the medullary centre of the temporo-sphenoidal lobe. At the same time the cingulum fibres make a rather thick plexus with the superficial fibres of the cornu Ammonis.

We have now reached the horizontal level below the frontal lobes, the last vestige of which has now entirely disappeared

The cingulum traced down to the level of the optic commissure maintains the same relation as before

We have now followed the posterior extremity of the cingulum as far as the horizontal level of the optic chiasma. It will now be necessary to revert to the anterior part of the cingulum, mention of which was made on p 148.

In the section made at the horizontal level of the upper part of the corpus geniculatum externum (fig 34, *Cing a*), the cingulum is seen as cut-across fibres lying in the gyrus fornicatus, in front of, and in immediate contact with, the genu of the corpus callosum. It forms a narrow oblong tract, whose direction is forwards and outwards, parallel to the genu of the corpus callosum

At its outer part some of its fibres seem to take an outward and forward direction into the frontal medullary centre, but this is not very definite. This appearance prevails till the horizontal level of the anterior commissure is reached, where the genu of the corpus callosum is very faintly represented, and only at its outer part. Below this level it is very difficult to make out the fibres of the cingulum, which seem to end here in a plexus

Attention must here be called to a narrow bundle of fibres which appears to be a part of the corpus callosum, and which is situated in front of the genu of this body, and is first seen at the level where this part of the corpus callosum begins to disappear. Its fibres are horizontal, and pass to the region of the cingulum forwards and outwards from the septum lucidum, or from the grey matter on the inner side of the lateral ventricle below the level of the genu of the corpus callosum. This bundle,

when seen in sections below this level and that of the lateral ventricle, can be traced outwards and forwards to mingle with the fibres from the extreme anterior end of the corona radiata, and then appears to pass on with them to the lowest frontal region.

Lower down still we reach a point where the fibres of the internal capsule have ceased, and this bundle of fibres still exists, and can be traced outwards to form an angle with the lowest anterior fibres of the corona radiata

When traced inwards at this level, it is found to end in the continuation of the septum lucidum below the lateral ventricle, for we have now reached a point which is inferior to the floor of the most anterior part of this cavity. When examined at the level where the last vestige of the frontal lobe is seen, it forms a very fine horizontal band of medullated fibres, bounding the anterior margin of the caudate nucleus

From the consideration of the above description, it would seem that the point, where the last trace of the anterior part of the cingulum can definitely be made out, is at the horizontal level of the middle of the anterior commissure, below which the characteristic appearance of the cut-across cingulum disappears, and its place is taken by a confused plexus, and partly by this bundle of fibres.

It seems, however, probable that this horizontal bundle of fibres in front of the corpus callosum ends externally in the cingulum, and at the place where this latter becomes indistinct, these fibres become more developed. Subsequently they take the place of the cingulum, and as we have seen, course outwards to mingle with the fibres from the corona radiata. They are certainly not part of the corpus callosum, as they do not pass to the opposite hemisphere, and the direction of the fibres is outwards and forwards, while that of the corpus callosum is more directly outwards. It therefore seems more likely that these are the extreme anterior fibres of the cingulum.

These are probably the fibres which can be seen in sagittal sections made nearest to the median line, as a layer of short horizontal fibres in front of the genu of the corpus callosum.

The above conclusion is borne out by sagittal sections of the Monkey, in which the fibres of the cingulum can be traced in the gyrus fornicatus round to the front of the genu of the corpus callosum, from which they are quite distinct. At the most anterior inferior part, the fibres of the cingulum have a direction downwards and backwards, and at right angles to those of the corpus callosum. They appear in short lengths, and are evidently proceeding in a plane which is oblique to that of the section, whereas the fibres of the cingulum in front of the point where the bend of the genu of the corpus callosum commences, have a direction almost vertically downwards, and consequently in horizontal sections these would appear as points, whilst the lowest fibres of the cingulum would be seen cut into short lengths. So here in the Marmoset the fibres of the cingulum in front of the genu of the corpus callosum appear in horizontal sections as points, whereas the fibres taking their place lower

down are cut more obliquely. Whether these fibres are part of the cingulum or not, they seem to connect the septum lucidum with the anterior inferior part of the frontal region

It has been considered by some writers, notably BROCA,\* that the cingulum forms one of the roots of the olfactory nerve, and it has been likened to the frame of a racket, which, forming a loop in the gyrus fornicatus and gyrus hippocampi, unites its two ends with the olfactory nerve, which thus forms the handle of the racket

In the present sections the first appearance of the roots of the olfactory nerve is not seen till we reach the last vestige of the frontal lobe, which is a very considerable distance from the definite termination of the cingulum, which as we saw, was at the level of the anterior commissure. There seems not sufficient evidence that the olfactory nerve can be traced to the part of the cingulum in front of the callosal genu, in horizontal sections

On referring to sagittal sections (p 146), it was shown that the termination of the descending posterior part of the cingulum takes place in the cortex of the inferior surface of the temporo-sphenoidal lobe, and that in the Marmoset the cingulum has not the connection with the olfactory nerve as described by BROCA

Having considered the cingulum in the sagittal and horizontal directions, I will continue with a description of it in the frontal, and also in the frontal oblique directions

*Frontal Sections.*—In making a frontal section (fig 39, *Cing h*) at the level of the optic commissure through the brain of the Marmoset, the cingulum is seen as a comma or pear-shaped bundle of fibres with the concavity towards the middle line, and with its general axis directed downwards and outwards, presenting the distinct appearance of fibres cut transversely

This bundle is situated at the lowest part of the internal angle of the centrum semi-ovale. Above, it is bounded by the rest of the centrum ovale, below and internally by the grey matter of the gyrus fornicatus (*GF*), and on its most inferior part the tail of the comma passes outwards and downwards, and then inwards, where it rests on the upper surface of the corpus callosum

The appearance of the transversely cut fibres is in marked contrast to those of the corpus callosum (*CC*), which sweep round its outer margin on their way to the cortex, and to the fibres from the internal capsule (*CI*), which pass upwards and inwards across the direction of the callosal fibres to end in the cortex. In this plane no fibres can be definitely seen to pass out from the cingulum into the cortex. Those fibres which do seem to come from the cingulum are really fibres from the corpus callosum or internal capsule, which pass through the cingulum, but are not connected with it.

As we pass from before backwards in these sections, the cingulum presents the same comma shape, but it gradually alters its position. The corpus callosum becomes

\* 'Revue d'Anthropologie,' 1878, "Anat Comp des Circonvolutions Cérébrales;" "Recherches sur les Centres Olfactifs," *ibid*, 1879

broader, and at the same time the gyrus fornicatus increases in the transverse horizontal direction, this has the effect of pushing the tail of the comma-shaped cingulum further away from the median line, so that the principal axis of its cross section instead of being almost vertical as in fig 39, becomes almost horizontal (fig 40, *Cing. h*) We therefore have the head of the comma forming the inferior median angle of the centrum semi-ovale, then passing almost horizontally outwards between the fibres of the corpus callosum above and the gyrus fornicatus below, and gradually tapering into its tail, which winds round the convexity of the most external part of the gyrus fornicatus and then runs inwards for a short distance along the upper surface of the corpus callosum with which it is in close contact. The most inferior end of the tail of the cingulum here comes into very close relation with a system of fibres which form the superficial fibres of the gyrus fornicatus (fig 40, *Sf*) These fibres are seen here as points along the inferior edge of a sulcus, which is the continuation of the dentate or hippocampal sulcus forwards in the gyrus fornicatus. The strip of cortex, which is separated from the rest of the gyrus fornicatus by this sulcus, rests on the upper surface of the corpus callosum, and at its outer part receives the tail of the comma-shaped cingulum, so that only the breadth of this strip of cortex intervenes between this part of the cingulum and the superficial fibres of the gyrus fornicatus.

Whether there is any communication between those two sets of fibres cannot be ascertained in frontal sections. On comparing the shape of the cingulum in figs. 39 and 40, the different appearances of the cingulum as seen in sagittal sections will be understood (see p. 144)

In the next series of frontal sections beginning at the vertical level through the anterior part of the pons Varolii, and extending backwards to the vertical level of the posterior part of the optic thalamus and the posterior end of the corpus callosum, the cingulum is still seen as a comma-shaped body having the same relations as before, but with its chief axis becoming more horizontal, the large end of the comma being directed inwards and the tail outwards and downwards, and with the fibres composing it cut across transversely.

In the last section of this series, viz., that opposite the level of the hinder part of the optic thalamus, the direction of the chief axis of the cingulum is quite horizontal. In all these sections it has not been possible to trace any fibres either entering the cingulum from the gyrus fornicatus, or passing into or out of the cingulum from the centrum ovale.

On considering the relation of the fibres leaving the cingulum to pass into the centrum ovale, it will be remembered that in sagittal sections (p. 145) these fibres pass out from the cingulum in a plane running forwards and upwards. The explanation is, I think, clear, why we do not see them in the frontal direction, as they would necessarily be cut across obliquely.

One of the most important points is that the cingulum, when traced forward to the vertical level of the optic chiasma and backwards to the vertical level of the hinder

part of the corpus callosum, does not vary in size, or, at any rate, does not become smaller as we advance forwards. This fact is very remarkable, as we see from sagittal sections that the cingulum continually gives off fibres upwards into the centrum ovale along its whole horizontal course in the gyrus fornicatus, and yet it does not diminish in size.

The fibres of the cingulum do not seem to be more closely aggregated together in these posterior frontal sections than in the anterior. It seems, therefore, reasonable to suppose that its fibres must be reinforced by continual additions, and it is suggested that these additions are received from the gyrus fornicatus.

As the cingulum can be traced into the temporo-sphenoidal lobe (in sagittal sections) we should expect to find it in this region in frontal sections. In looking at preparations made in the frontal direction through the temporo-sphenoidal lobe, the cingulum is seen as a tract of cut-across fibres lying superior to, but in contact with, the central white matter of this lobe (fig 40, *Cing*, *p*), and it here forms a bulbous enlargement.

Fine fibres can be seen passing across the grey matter between the cingulum and the superficial fibres of the gyrus hippocampi (the external medullated layer of the cornu Ammonis). This condition is maintained as we pass backwards until we reach the region behind the level of the pons and medulla.

Another series of sections were taken through the right half of a Marmoset's brain, which was cut in a fronto-oblique plane, beginning in front through the most anterior part of the pons Varoli, and extending backwards to the middle of that part and the posterior extremity of the lenticular nucleus.

In these sections the cingulum appears as a comma-shaped collection of transversely-cut fibres situated at the extreme inner and inferior angle of the centrum semi-ovale.

A few fine fibres issue from the upper part of the cingulum into the gyrus fornicatus, but they seem to be passing through the former from the centrum ovale on their way to the cortex, and do not actually take their origin from the cingulum.

In these sections the cingulum keeps the same size, and does not vary as we pass either in an anterior or posterior direction.

In a further fronto-oblique section, which was taken at the level through the posterior part of the corpus callosum above and the fourth ventricle below, the cingulum is seen in the gyrus fornicatus, having a similar appearance to that already described in the other fronto-oblique sections.

In the temporo-sphenoidal lobe, the cingulum (the third or posterior part) can be distinguished as a pyramidal-shaped collection of fibres, lying above and in contact with the central white matter of this lobe. The cingulum is here so involved with the fibres of the alveus (the prolongation of the fimbria from the fornix) that it is difficult to separate them (see sagittal sections, p 147).

In the next sections (fig 42, 43, right) made through the most posterior part of the corpus callosum and the corpora quadrigemina, the cingulum fibres (fig 43, right *Cing*, *p*.) are seen as part of a projection of white matter upwards into the gyrus



hippocampi, which is separated off on the inner side from the projection of the central white matter of the temporo-sphenoidal lobe, by a fissure which here seems to spring from the hippocampal or dentate sulcus (*HS*), this is the commencement of that most important fissure, the calcarine (*F' C*) We have, therefore, the white matter here forming a U-shaped collection of fibres round the calcarine fissure The limb of the U containing the cingulum is external, and superior to the calcarine fissure, and is composed of two parts, the inner part nearer the middle line is formed by the calcarine fibres (fig. 43, right, *Cf*), whilst the outer part, which bounds inferiorly the cornu Ammonis, shows fibres cut across and is the cingulum (fig. 43, right, *Cing.*, *p.*)

It will now be advisable to explain more minutely the relation of the calcarine fibres to those of the cingulum At first it might appear as if the cingulum extended from the inner lip of the calcarine fissure round to the outer lip and so up the isthmus of the gyrus fornicatus, but on examining sagittal sections (figs. 10 and 11), and horizontal sections (figs. 35, 36) it is seen that the cingulum never becomes inferior or posterior to the calcarine fissure Further, it will be remembered that the sections (figs. 41-45) which we are now examining, are not frontal but fronto-oblique. Consequently, a section made at this level would pass inferiorly through the occipital lobe—this is shown by the fact that we have now reached the point where the calcarine fissure appears in sagittal sections to pass backwards from the dentate sulcus—and would therefore cut through the cingulum somewhere in the upper part of the gyrus hippocampi, or in the isthmus of the gyrus fornicatus (fig. 10, near *S.f.*). We have here, therefore, the calcarine fissure becoming more marked as we proceed backwards, whilst the dentate sulcus diminishes and finally disappears. Passing therefore round the bottom of the calcarine fissure there is this U-shaped set of fibres, viz., the calcarine (fig. 41-45, *Cf*)

At the bottom of the U, and extending upwards along its outer limb, the cingulum is seen (fig. 43, right, *Cing.*, *p.*) as a conical collection of fibres projecting upwards into the gyrus hippocampi and helping to form the outer limb of the U-shaped calcarine fibres It is particularly to be noticed that the cingulum is represented by these conical fibres only, the rest of the U being calcarine. This appearance was referred to in horizontal sections, where the separation between the calcarine and cingulum fibres can be better understood (p. 150).

The direction of the fibres composing this outer limb is also different, the calcarine fibres having a course downwards and inwards to reach the bottom of the U, whereas those of the cingulum are irregularly cut across

An important change has now taken place (fig. 42, left) between the relation of the gyrus hippocampi to the gyrus fornicatus, this latter has gradually become prolonged downwards along the median face of the hemisphere, and it finally reaches the gyrus hippocampi and joins it, forming the isthmus of the gyrus fornicatus.

The hippocampal or dentate sulcus now changes its direction, the inner end becoming the superior, so as to be parallel with and external to the gyrus fornicatus. We have,

therefore, the gyrus fornicatus and gyrus hippocampi forming a continuous convolution, having the projection of the cingulum at its lower part, and separated on its outer surface from the fascia dentata by the hippocampal or dentate sulcus (*cf* fig 44, left, *H.S* )

The change in the position of the dentate sulcus will be more easily understood if we look upon the junction of the gyrus hippocampi and gyrus fornicatus as a growing upwards of the former to join the latter.

On fig 45, right side, the two convolutions are still separated and the calcarine fissure (*CF*) is seen to be formed by two lips, an upper and a lower, containing a U-shaped collection of fibres, the upper one is bounded above by the hippocampal or dentate sulcus (*HS*), which proceeds from the free median edge of the gyrus hippocampi into the substance of this structure. If now this upper lip were to be prolonged upwards till it joined the gyrus fornicatus (*GF*) the hippocampal sulcus would have its inner end carried upwards, and its direction would be changed from being almost horizontal (*H.S* in fig 45, right) to one parallel to the isthmus of the gyrus fornicatus, where it would bound this structure on its outer side separating it from the fascia dentata (*H.S.* in fig 44, left).

As we proceed more posteriorly the cingulum comes into relation with the forceps major (fig 41, left, *FM*), which here extends to the floor of the descending ventricular cornu and bounds the cingulum on its outer side, at the same time the U-shaped tract of the calcarine fibres becomes larger as the calcarine fissure increases in depth. Its fibres have now the following direction: when traced from the tip of the inner limb of the U they are here connected with the cortex and have a direction down and out parallel to the limb of the U, but on reaching the outer horn they have a direction outwards and upwards.

In the next sections (figs 42-44, left) where the gyri hippocampi and fornicatus have joined, the U-shaped tract increases in size and its outer and upper horn is prolonged up the isthmus of the gyrus fornicatus, carrying the cingulum (*Cing p*, fig 44, left) up with it, while at the same time the fibres of the forceps major diminish in size and finally disappear from this part.

Up to this point (fig 45, left) there has been no alteration in the fibres of the horizontal cingulum (*Cing. h*), situated in the gyrus fornicatus on the under surface of the centrum ovale. These fibres have been already described in frontal sections further forward, as having the shape of a comma and presenting transversely cut fibres.

In more posterior sections they begin to have a direction downwards into the gyrus fornicatus, *i.e.*, towards the centre of the circle of which the comma is an arc. By this time the posterior cingulum has advanced up the isthmus of the gyrus fornicatus and in the next section its fibres join the comma-shaped fibres of the horizontal cingulum above, so that eventually we have the whole of the concave part of the "comma" completely filled up by the fibres of the cingulum which have been traced up the gyrus fornicatus. We thus get instead of the "comma," a collection



of fibres shaped like a bulb (see sagittal and horizontal sections), of which the stalk is formed by these fibres from the isthmus of the gyrus fornicatus

We have therefore traced the posterior part of the cingulum up through the isthmus to the posterior extremity of its horizontal part on the inner and under side of the centrum ovale, where it forms the bulbous enlargement which was also seen in the sagittal and horizontal planes

The question as to how many of these fibres, which are seen in the gyrus fornicatus below the bulbous enlargement, belong to the cingulum and how many to the calcarine fibres, it is difficult if not impossible to answer. A glance at a sagittal section in which the cingulum is seen through the whole of its posterior part (fig 11, *Cing. p*) will show that a fronto-oblique section, sloping as it does downwards and backwards, through the upper end of the cingulum would include only a small portion of its cross-section and the rest of the fibres in the gyrus fornicatus, and the cortex forming the upper lip of the calcarine fissure would be calcarine fibres, it seems probable therefore that only the fibres immediately below the bulb belong to the cingulum, the rest being part of the calcarine fibres which here have the following arrangements

Starting below in the white matter of the occipital convolution below the calcarine fissure, the fibres spring apparently from its cortex and pass horizontally outwards along the direction of the tract to the part forming the bottom of the calcarine fissure, where they appear in short lengths. The fibres directly external to the bottom of the calcarine fissure are cut obliquely and their precise direction cannot be ascertained, but it appears to be outwards and upwards, across the direction of the tract.

The fibres issuing from the bulb of the cingulum downwards, and which probably belong to the cingulum, have a straight course for a short distance, tapering as they proceed, but whether they end in the cortex of the isthmus of the gyrus fornicatus cannot be definitely ascertained. These fibres, when traced to the periphery of the bulb, end abruptly and probably run forward.

This bulbous enlargement is bounded on the outer side by the corpus callosum, above by the centrum ovale, and on its inner side by the cortex of the gyrus fornicatus.

In the next sections the bulbous enlargement has disappeared, as we are now posterior to it, and in its place we find that the fibres which are seen in the upper part of the superior calcarine lip pass upwards along the inner side of the centrum ovale, and instead of ending abruptly they pass on and turn upwards into it. In further posterior sections there are two layers of these fibres, an inner which is directed towards the highest point of the centrum ovale, and an outer next to the corpus callosum, which winds round the upper end of this structure into the centrum ovale on the outer side of the posterior ventricular cornu. It is considered that, as this appearance is continued with slight modifications in the rest of these sections which reach for some distance into the occipital region, these fibres cannot be part of

the cingulum which, as we saw in sagittal sections, does not extend into the occipital region, but form part of the calcarine system of fibres

Whether these fibres arise at their lower end from the cortex forming the superior calcarine convolution (or upper lip of the calcarine fissure) is not certain, but they appear to do so.

We thus have a system of fibres which can apparently be traced (the system, not the individual fibres) from the tip of the central white matter in the temporo-sphenoidal lobe round the convolution bounding the bottom of the calcarine fissure, and up the superior limb of this convolution to its continuation on the median surface of the hemisphere. There it winds round the inner side of the lateral ventricle and the corpus callosum, and turns upwards and outwards into the white matter of the hemisphere, the centrum ovale

*Summary* — Having followed the fibres of the cingulum in consecutive sections in the different planes, it will now be advisable to try and combine the different appearances seen.

To facilitate the description of the cingulum it will be, as before, divided into three parts —

1st The horizontal, lying above the corpus callosum.

2nd. The anterior, extending in front of the corpus callosum

3rd. The posterior, extending from behind the splenium of the corpus callosum to the anterior part of the temporo-sphenoidal lobe

1st. The horizontal. The horizontal part extends from the isthmus of the gyrus fornicatus behind to the anterior part of the corpus callosum in front. On transverse section it has the form of a comma, with its concavity towards the middle line and towards the gyrus fornicatus. On its outer side is the centrum ovale and the corpus callosum, along which its tail extends to the under surface of the gyrus fornicatus. Its fibres rise posteriorly from the cortex of the isthmus of the gyrus fornicatus (sagittal sections). They then pass upwards and forwards from behind the splenium of the corpus callosum, and turn upwards and outwards into the centrum ovale. Along the whole of this horizontal part fibres are being continually given off into the centrum ovale, into which they can be traced through half of its vertical depth. The most anterior of these are nearer to the middle line than the posterior.

The cingulum in this part, therefore, consists of a series of fibres having a direction forwards and upwards, and which run for a short distance only along the cingulum. There is no doubt that the anterior end of each individual fibre passes into the centrum ovale. With regard to their posterior ends the origin is not so clear, as, with the exception of the isthmus, no definite connection can be made out between the under or inner surface of the cingulum and the cortex of the gyrus fornicatus.

At the anterior part the (horizontal sections) cingulum sends fibres outwards, and also some round the genu of the corpus callosum to the centrum ovale.

2nd. The anterior part of the cingulum in front and below the genu of the corpus

callosum appears in sagittal sections to consist of fibres which, arising from the most anterior part of the centrum ovale, pass downwards and backwards and thence into the internal root of the olfactory nerve. The direction of the fibres is here in the opposite direction to what it is in the horizontal part, if the cingulum were extended, so to say, in a straight line, though these fibres are described as part of the cingulum, it must be remembered that in horizontal sections the direct continuity of the fibres could not be traced lower than the level of the anterior commissure. It is therefore doubtful whether this part really belongs to the cingulum system.

3rd The posterior part of the cingulum extends from behind the splenium of the corpus callosum to the anterior part of the temporo-sphenoidal lobe.

The tract of fibres as it descends in the isthmus of the gyrus fornicatus becomes further removed from the middle line, and gradually gets behind the hippocampus major, where it becomes flattened in the horizontal transverse direction. Lower down its transverse section appears more round, and as it becomes horizontal in the temporo-sphenoidal lobe its section is more triangular, with the apex upwards.

At first its fibres come into close relation with the calcarine fibres, from which they are not easily separated (see p 162). These calcarine fibres lie behind those of the cingulum as far down as the level of the inferior surface of the occipital lobe.

The cingulum, in passing into the gyrus hippocampi behind the cornu Ammonis, still keeps posterior and internal to the forceps major (horizontal sections, fig. 37), and at the level below the calcarine fissure the most external fibres of the cingulum are traversed by the latter on their way to the cortex below the calcarine fissure (sagittal sections).

The relation of the cingulum at this level (*i.e.*, just below the horizontal level of the calcarine fissure) to the neighbouring grey cortex is not very definite, as no connection can be traced either into the gyrus hippocampi in front of it, or to the cortex below the calcarine fissure behind it (sagittal). In the temporo-sphenoidal lobe the cingulum runs downwards and forwards in the gyrus hippocampi. Its constituent fibres run obliquely downwards; they receive offsets from the superficial fibres of the gyrus hippocampi on their upper surface, and they end in the cortex on the inferior surface of the temporo-sphenoidal lobe. It is to be remarked that, whilst the fibres which can be traced from the part of the cingulum which is at a level superior to the calcarine fissure, end in the cortex of the inferior part of the temporo-sphenoidal lobe, that part which receives offsets from the superficial fibres ends in the cortex at a point further forwards. Further, the superficial fibres from the most anterior part of the cornu Ammonis (see fig 11) run forwards in the most anterior part of the cingulum, where it forms a leash of fibres, which end in the cortex of the under surface of the tip of the temporo-sphenoidal lobe, it is quite certain that none of these fibres turn upwards to end in the nucleus amygdalæ, and they certainly do not go towards the locus anterior perforatus.

The cingulum here consists of layers of short fibres, having a direction downwards

and forwards, coursing between the cortex of the gyrus hippocampi and that of the temporo-sphenoidal lobe.

The arrangement is somewhat similar to what was seen in the horizontal part of the cingulum, with this difference that, whereas in the latter the individual fibres ran forwards and upwards, here they run forwards and downwards. It therefore seems probable that in both cases they form a connecting system between the gyrus fornicatus and the gyrus hippocampi on the one hand and the centrum ovale (? cortex on external surface) and the cortex of the temporo-sphenoidal lobe on the other.

Similarly to what was seen in the horizontal part of the cingulum, its transverse diameter does not vary much throughout its extent in this part, but owing to the difficulty of separating it from the calcarine fibres, this point is not certain.

In reference to the functions of the cingulum and the arrangement of its fibres, I have in one case tried to cause degeneration in its fibres.

To produce this, I asked Professor HORSLEY to perform the operation in a Monkey (*Macacus sinicus*) of dividing the cingulum in its horizontal course through the gyrus fornicatus. The operation was done under an anæsthetic, and with strict antiseptic precautions, by means of a blunt hook introduced along the median surface of the left hemisphere after gently drawing it away from the middle line. The place chosen was at the junction of the quadrate lobule with the horizontal part of the gyrus fornicatus, and therefore just below the angle which the calloso-marginal sulcus makes when it changes its direction from downwards and forwards to horizontally forwards. The animal lived for two months after the operation, and on examining the brain it was found that at the median surface the cut extended through the whole width of the gyrus fornicatus, but in sections made external to the median line, although the whole extent of the convolution was not cut through, the fibres of the cingulum were completely severed. After hardening the brain, serial sections were made in the sagittal direction, beginning from the median line and passing outwards to the vertical level of the outer part of the head of the caudate nucleus. After staining the sections with PAL'S method, on examining the cingulum in front of, and behind the cut, the following appearances are seen.—The gap left by the operation is filled up near the middle line by a slight amount of cicatricial tissue, but there is no evidence of any inflammation, showing that the wound had healed by first intention. In front of the cut the fibres of the cingulum end abruptly at their posterior ends, and although there is the appearance of injury to the ends of the fibres, no degeneration can be traced along their continuity forwards, there is no change in the staining of the myeline sheath.

Posterior to the cut, the fibres of the cingulum can be traced forwards to where they have been cut across. Degeneration is seen to have taken place at the margin of the cut, and on tracing these fibres backwards they are found to be slightly degenerated for a considerable distance backwards, but whether the change in each fibre extends through the whole length of its course cannot be made out. There is,

however, a marked difference between the fibres at the inferior part (*i.e.*, that next to the corpus callosum) of the cingulum, and those more superior (*i.e.*, nearer to the calloso-marginal sulcus), these latter were not cut across, as they turned upwards before reaching the seat of operation, and consequently they are not degenerated, and their individual fibres can be made out very well, but in the former, under a high power (F, ZEISS), there is a considerable amount of degeneration, which extends some way backwards

From this one experiment it would appear that the cingulum, when cut across, does not degenerate forwards, but any change takes place in a posterior direction. Further that it is not possible even after cutting the cingulum completely across to produce degeneration in all its fibres. This is in harmony with the arrangement of the fibres as seen in sagittal sections of the Marmoset, and confirms the opinion there expressed that the cingulum does not contain fibres running through its whole length, but is made up of relays of fibres which are continually leaving it.

It should be stated that after the operation no change could be detected in the animal operated on, there was no paralysis and no evidence of any loss of sensation, though it was carefully tested.

On comparing this description of the cingulum with the account given by various authors on human anatomy, it would seem that, although communications have been traced along the annectant gyri from the cingulum to other convolutions, they are described by FOVILLE and HUGUENIN (p. 142) as *fibræ arciformæ* and resemble the *fibræ propriæ* of other parts. In the Marmoset, on the other hand, the fibres of the cingulum have a definite direction; they are quite distinct from the superficial *fibræ propriæ*, and with the exception of the calcarine fibres, they have an arrangement special to themselves—they end deeply in the centrum ovale, and are not part of the superficial connecting fibres of the cortex.

The peculiar arrangement of the cingulum in the gyrus fornicatus is of especial interest, when considered with the fact found out by Professors HORSLEY and SCHAFER,\* that whereas the marginal convolution was excitable, no movement was produced when the gyrus fornicatus was stimulated electrically, and moreover that loss of sensation on the opposite part of the body was produced in Monkeys when parts of this convolution were removed, thus showing that it was associated with the function of sensation. It is here suggested that in the Marmoset the cingulum may form internuncial fibres between the gyrus fornicatus—the sensory part of the cortex—and the part of the centrum ovale in connection with the so-called motor cortex.

*\*Calcarine Fibres.*—In describing the cingulum frequent allusion has been made to a system of fibres which I have called calcarine, from the fact that they are found in that part of the cortex which is involuted to form the calcarine fissure.

In all the different planes (especially sagittal and horizontal) great difficulty was

\* 'Phil. Trans.' B., vol. 179 (1888).



found (figs 5, 22, 23, *Cing p*, *Cf*) at the junction of its horizontal and posterior parts to find the limit of the cingulum in the posterior direction. It was seen to be merged into a set of fibres which could be traced into the occipital region along the most superficial part of the white matter in the cortex bounding the calcarine fissure. It was not till sections were made in the fronto-oblique direction that the relation of these fibres became more evident. It was then seen that posterior to the vertical level of the horizontal part of the cingulum there was a U-shaped layer of fibres (figs 41-45, *Cf*) in the occipital region, maintaining an analogous position to that of the cingulum further forwards. In more posterior sections the direction of these fibres at the superior part was from the cortex forming the upper lip of the calcarine fissure upwards, forwards, and outwards round the inner side of the tapetum into the centrum ovale, the fibres bounding the lowest part of the calcarine fissure had a direction in horizontal sections (fig 38) backwards and outwards from the cortex of the inferior lip of the calcarine fissure, while those in the inferior lip of the calcarine passed from the calcarine cortex downwards and outwards (fig 44, left). In figs 1, 2, all the occipital fibres are calcarine, with a direction forwards and upwards.

It is therefore probable that these calcarine fibres form a connecting system between the cortex bounding the calcarine fissure and the centrum ovale. Moreover the fibres stain (with WEIGERT'S method) a tint similar to that of the cingulum, it is therefore probable that the two systems are analogous, *i e*, association—or collateral—fibres which connect the centrum ovale with the gyrus fornicatus and the cortex bounding the calcarine fissure, respectively, for like the cingulum the calcarine fibres appear as relays, and no one fibre can be traced from the tip of the inferior lip continuously through the whole tract to the centrum ovale. Another remarkable point is the manner in which the calcarine fibres hedge off their cortex from surrounding parts, apparently even from the corpus callosum (see p 180).

*Superficial Fibres of the Gyrus Fornicatus*—In the description of the cingulum frequent reference has been made to the superficial fibres of the gyrus fornicatus. It is not here intended to follow out the whole course of these fibres, but it will be advisable to refer to them as they come into relation with the cingulum.

These fibres are seen having an antero-posterior direction at the most inferior part of the gyrus fornicatus (fig. 4, *Sf*) in sagittal and also in frontal sections (fig. 40, *Sf*), and in the latter plane they appear to come into very close relation with the cingulum.

It has been already stated (p 140) that in the Marmoset the dentate or hippocampal sulcus is prolonged from the gyrus hippocampi along the horizontal part of the gyrus fornicatus, and can be traced as far as the frontal level of fig 39, and probably in front of this point. In frontal sections (fig 40) this prolongation of the dentate sulcus is seen passing outwards from the median line into the gyrus fornicatus, and cutting off a very narrow strip of grey matter (indusium griseum) next to the superior surface of the corpus callosum. It is in the outer part of this strip, where it is attached to the rest of the gyrus fornicatus and along the edge of the dentate sulcus,

that these superficial fibres are seen, having a horizontal antero-posterior direction, but though they come into close contact with the tail of the comma-shaped cingulum, they are separated by a strip of cortex, and no fibres can be here seen to pass between them. When traced backwards along the edge of the gyrus fornicatus these fibres pass to the isthmus, always keeping along the edge of the dentate sulcus, which now separates the fascia dentata from the commencing gyrus hippocampi (figs 5, 29, *Sf*). The fibres in the isthmus have an antero-posterior direction parallel to the free cut surface of the gyrus fornicatus (fig 5), and fibres radiate towards them from the bulb-shaped posterior end of the horizontal cingulum, but it is uncertain whether they join. The superficial fibres then descend to the edge of the gyrus hippocampi which forms the posterior inferior lip of the hippocampal sulcus (figs 10, 35, 38, *Sf*, *H.S*), they keep parallel to the cingulum, and just in front of it. They descend to the lower end of the gyrus hippocampi where they end in a plexus. Along this part of their course, offsets are given downwards and forwards to the cingulum, the main part of which they form at its inferior end (figs 11, 12, *Sf*). It will be observed that these fibres now form what is known in the cornu Ammonis as the external medullated layer, Kernblatt, or lamina medullaris involuta. When they are traced upwards in sagittal sections (fig 11, *Sf*), they end in a fine plexus at the upper end of the gyrus hippocampi, where they come into contact with the protoplasmic processes of the large cells of the pyramidal cell layer of that gyrus.

The superficial fibres of the gyrus fornicatus have been described by SCHWALBE\* and other authors as part of the cingulum, but whether this is correct or not, they certainly have a course which is distinct from this structure, while it is only in the gyrus hippocampi that a connection between the two sets of fibres can definitely be made out.

In connection with this matter it is interesting to note the manner in which the cornu Ammonis or hippocampus major is formed. In horizontal sections (fig. 16, *F'D*, *Cing p*) the fascia dentata is slightly seen on the anterior edge of the dentate sulcus and on its posterior edge a faint line shows the superficial fibres, while the cingulum is seen behind and outside the sulcus. If now we imagine the superficial fibres to be pushed, so to say, outwards together with the dentate sulcus into the substance of the gyrus hippocampi, and at the same time the cingulum to extend inwards into the outer surface of this gyrus until the two sets of fibres overlap each other, the cingulum being the posterior, we get the appearance of the cornu Ammonis gradually produced, as seen in figs 23-34, and more marked still in figs. 35-38 (*H.S*, *Sf*, and *Cing p*), and thus the sigmoid form is brought about by the gradual extension of the superficial fibres and the cingulum in opposite directions into the gyrus hippocampi.

Having finished the account of the cingulum, the posterior part of the corpus callosum will now be described.

\* *Loc. cit.*



*Posterior Part of the Corpus Callosum*

*Previous Descriptions*—According to QUAIN'S 'Anatomy' (9th edit), vol 2, p 344, "From the posterior end, or splenium, of the corpus callosum they (the fibres) arch round the posterior and inferior cornua of the lateral ventricle, forming the upper and outer wall of those parts of the cavity, into the temporo-sphenoidal and the lower part of the occipital lobes. Lastly, from the under part of the splenium fibres pass with a bold sweep (forceps major) into the posterior and superior parts of the occipital lobes."

The forceps major is further on (p 346) described as forming a longitudinal eminence (bulb of the posterior cornu) on the inner wall of the posterior cornu of the lateral ventricle, where the fibres of the forceps major curve round from the splenium of the corpus callosum to enter the occipital lobe.

SCHWALBE\* states that the hinder part of the body of the corpus callosum and its splenium are destined for the temporal and occipital convolutions. "The fibres from the posterior part of the body run laterally and inferiorly in an arch, convex outwards, and course in the upper lateral wall of the posterior and inferior horns of the lateral ventricle as a thin layer of white matter, being only covered over by the ependyma, and called the tapetum. This structure contains the callosal fibres for the temporal and the inferior part of the occipital convolutions. The swelling formed on the under surface of the callosal body by the rolling under of the fibres—the splenium proper—sends its fibres to the posterior and upper part of the occipital convolutions in such a way that the latter are supplied by the callosal fibres coming from the angle formed by the splenium with the body, while the posterior part of the occipital gets its callosal fibres from the splenium itself. The arrangement on each side of these concavely-shaped tracts from the splenium forms what is known as the forceps major posterior. It will be seen that, as the splenium is attached directly to the corpus callosum so the forceps major is in immediate contact with the tapetum, and represents the portion of the tapetum which is rolled up towards the middle line."

According to HENLE,† "the fibres from the splenium which bend round into the posterior extremities of the hemispheres are called by REIL 'the forceps;' the fibres radiating out of the body of the corpus callosum form the *tapetum*." "The outer wall (*loc. cit*, p 147) (of the lateral ventricle) which is concentric with the surface of the hemisphere, and forms the upper and lateral boundary of this cavity, is identical with the tapetum, it begins at the posterior edge of the thalamus, with a concave base corresponding to the height of the outer wall, and gradually diminishes from before backwards, till finally it ends as a fine point." "The median wall (*loc. cit.*, p 148) of the posterior horn is formed by 'the forceps,' this forms a longitudinal fold or projection into the cavity of the posterior cornu, and is called *bulbus cornu*

\* 'Lehrbuch der Neurologie,' p 494 1881

† 'Handbuch der Anatomie des Menschen,' p 146 1868

posterioris, and becomes deeper from before backwards, and, as the floor narrows, we finally have only a semilunar-shaped furrow in the tip of the occipital lobe ”

OBERSTEINER\* states “that it is probable that the corpus callosum sends fibres to the whole surface of the cerebrum, with the exception of the inferior and anterior parts of the temporo-sphenoidal lobes and the olfactory regions (tractus olfactorius).”.

“ From the splenium corpus callosi a large white mass of fibres, the forceps posterior, run backwards to the posterior part of the central hemispheres, having their convexity towards the middle line. The thick tracts of white fibres which are given off from the posterior part of the body of the corpus callosum are directed for the most part downwards, and form the lateral wall of the posterior and inferior parts of the lateral ventricles ”

*Sagittal Sections* —Before proceeding to the description of the posterior part of the corpus callosum, it should here be remarked that there seems some difference of opinion among the authorities as to the definition of the word “ splenium.” According to QUAIN,† the whole of the posterior end of the corpus callosum is called the splenium, whilst the part which is rolled under, called the “ bourrelet ” or pad, is termed the under part of the splenium.

On the other hand, SCHWALBE‡ describes the rolling under of the posterior part of the corpus callosum as the splenium. He qualifies this on the next page by stating that the splenium proper is the swelling rolled round towards the front on the inferior surface of the corpus callosum.

HENLE§ again makes a difference between the splenium, which gives off the fibres known as the forceps, and the posterior part of the body of the corpus callosum, which gives rise to the radiating fibres forming the tapetum.

The corpus callosum will be here described as consisting of three parts, the *posterior part of the body*, which gives rise to the tapetum; the *splenium proper*, or the part rolled under the former, from which springs the forceps major posterior; and an *intermediate part*, connecting the splenium proper to the body of the corpus callosum.

*Sagittal sections* —The corpus callosum presents at the median line a thickened posterior end; on the under surface of this there is an oval collection of fibres having the smaller end forwards—this oval is the splenium proper, and it is separated off from the rest of the corpus callosum by a septum into which the median fibres of the fornix can be seen to pass (see p. 182). The direction of the callosal fibres is transverse to the plane of the section.

The corpus callosum and its splenium are so fitted together that the whole presents at the median line a uniform contour.

\* *Loc. cit.*, p. 345.

† *Loc. cit.*, p. 344.

‡ *Loc. cit.*, p. 493.

§ *Loc. cit.*, p. 146.

In succeeding sections, on examining the posterior part of the corpus callosum, it (fig 1, *CC*.) consists of a rounded thickened end, and attached to its lower part is the oval collection of fibres of the splenium proper, which is separated off from the main part of the corpus callosum by a septum, which appears in fig 1 as a slight interval, and into this septum the fibres of the median part of the fornix still enter (*F.m*, see p 182) In the next sections this septum passes upwards into the substance of the corpus callosum, and detaches its most posterior end from its main part, leaving them in connection only at their upper parts

We have here, therefore, the posterior end of the corpus callosum presenting three different parts, viz, the posterior part of the body (fig 4, *CC*); below this, and separated by a septum, is the splenium proper (*spl*), and joining the splenium proper to the main part of the corpus callosum are the fibres (*spl'*), which, attached to the posterior-superior part of the splenium below—a slight fibrous septum intervening—and above to the posterior-superior angle of the main part, form an intermediate portion between the corpus callosum and its splenium. It is to be observed that the median fibres of the fornix pass into the corpus callosum in front of this intermediary part. In all these callosal fibres the direction is transverse to the plane of the section

In more external sections the axis of this intermediary part of the splenium, which here appeared vertical, becomes more oblique, so as to slant backwards and upwards. The posterior part of the body soon begins to send fibres backwards into the occipital region, which cut through the outer part of the cingulum, and in the next section this intermediate part of the corpus callosum becomes still more inclined backwards, and also sends fibres backwards into the occipital region, lying beneath those from the posterior part of the body

The prolongations backwards from these two parts of the corpus callosum are so closely connected that it is difficult to separate them, and it is not till we arrive at a more external section that a distinct differentiation can be made out. Here (fig 5, *CC*, *Spl'*) the fibres from the intermediate connecting part of the corpus callosum can be seen arising rather abruptly between the splenium proper (*Spl*) and the body, and passing backwards and then upwards into the occipital region, where they form a leash of fibres distinct from the prolongation backwards from the posterior part of the corpus callosum, along whose under surface they course, they lie on the bulbous enlargement of the cingulum and the calcarine fibres (fig 5, *Cing p*, *Cf.*), which separates them from the cortex forming the upper lip of the calcarine fissure. The arrangement of these two parts of the callosal fibres is better explained in fronto-oblique sections (*q.v*)

In the next section of the series (fig 6) these fibres from the intermediate part of the corpus callosum, are separated off from the main body by the lateral ventricle, whose posterior cornu here begins to be formed. Here, also, these fibres become very closely applied to the bulbous enlargement of the cingulum (see p. 146), so that they

are free on their upper surface towards the lateral ventricle, while inferiorly they are bounded by the cingulum and the calcarine fibres. They can still be traced from between the splenium and the corpus callosum in front, where their fibres are arranged in short cut bundles, to the end of the posterior cornu of the lateral ventricle behind. Here the fibres have a distinctly horizontal antero-posterior direction, and do not present the short lengths seen more anteriorly. When traced posteriorly they end between the fibres from the body of the corpus callosum and the calcarine fibres, and blend finally with the former. In more external sections (figs 8 and 9), the posterior part of these fibres disappears, while the portion of them in front of the cingulum still exists. As will be seen further on, these fibres in front of the cingulum are the commencing forceps major from the splenium.

We must return to the splenium, which was described as an oval structure below the body of the corpus callosum. As we proceed further outwards the following changes occur (fig. 5), the splenium (*Spl*) becomes more triangular, and forms a wedge-shaped bundle of cut-across fibres with the apex downwards. It lies between the optic thalamus (*O.T*) in front, and the commencement of the fascia dentata (*F.D.*) behind. At its upper part it is separated from the main body of the corpus callosum by the median fibres of the fornix.

In the next section (fig 6) the shape of the splenium has become more wedge-shaped, and its fibres are arranged in distinct bundles.

We have now (fig. 7) in the occipital region the following set of fibres from above downwards. Beginning with the cortex of the outer superior surface of the occipital lobe we have, first, the sub-cortical plexus of fibres of the centrum ovale; next, below them, the fibres coming from the posterior part of the internal capsule (*C.R.*), with probably some of the optic radiations of GRATIOLET, which have a direction upwards and backwards, below them the fibres from the hinder part of the corpus callosum (*C.C.*), which are quite distinct, and are bounded in front by the caudate nucleus, while behind they end in a long narrow tail of fibres, which, diminishing as they extend backwards, can be traced to the posterior part of the occipital lobe (figs 9, 10, *Tap.*). The arrangement of the fibres is at first so irregular that no definite direction can be made out, but in the tail it is downwards and backwards, thus making a sharp angle with those from the internal capsule.

The posterior part of the corpus callosum has here a semi-pyriform shape, the large end being forwards and the smaller end of the pear being posterior, where it forms the long tail of fibres. It is bounded above by the corona radiata, in front by the caudate nucleus, and inferiorly by the posterior cornu of the lateral ventricle, which here separates it from its splenium and from the calcarine fibres (fig. 10, *C.f.*). This prolongation of the corpus callosum backwards into the occipital lobe is what is known as the tapetum, and its relations will be better understood by referring to the description of the corpus callosum in the horizontal direction. At present it will suffice to note that there is no connection between these fibres of the corpus callosum

and those of the internal capsule, as has been stated by Professor HAMILTON ('Roy Soc Proc,' February, 1884), in fact, the two sets of fibres are at an acute angle to each other

We must now consider the relation of the splenium to the posterior part of the corpus callosum. In fig 5 (*Spl*) the splenium is of a triangular shape, and is, so to speak, wedged in between the optic thalamus in front and the fascia dentata behind. At its anterior and upper angle are the fibres of the fornix, *i.e.*, the posterior descending crus (*F<sub>l</sub>*), which forms the tænia hippocampi. Here, therefore, the splenium is in close proximity to its main body. In the next section (fig 6), however, the posterior part of the corpus callosum is seen to be separated from its splenium by a distinct space. This space is the commencement of the posterior horn of the lateral ventricle, and is very well seen in fig 7.

The posterior part of the body of the corpus callosum is therefore above the lateral ventricle, whilst the splenium is below it, and, as will be more apparent in horizontal sections (p 175), the splenium supplies parts on the inner wall of the ventricle.

On examining the triangular collection of fibres of the splenium their arrangement is not uniform. At the upper or thicker end of the wedge the fibres are transversely cut across and arranged in large bundles, loosely packed together, whereas, at the apex of the wedge, the fibres are much less stained and are packed closer together. Moreover, the latter receives the fibres of the fornix which eventually form the tænia hippocampi (see p 183). This arrangement into two sets of fibres is very important, as the subsequent course will show.

As we proceed further outwards the fibres of the main body of the corpus callosum do not alter much, except that the tapetum can be traced for a further distance into the occipital region.

The deeply stained fibres of the upper part of the wedge, which are evidently the fibres of the splenium, or, as they must now be called, the forceps major posterior, *i.e.*, the continuation of the splenium backwards and outwards, pass gradually backwards over the superior surface of the hippocampus major and become much thicker, so that in fig 11 there is the following arrangement at the upper end of the hippocampus major — In front we have the posterior pillar of the fornix (*F<sub>p</sub>*) on its way to form the tænia hippocampi, and here stained brown colour (WEIGERT); above, the deeply stained fibres of the forceps major (*F<sub>M</sub>*) arranged in large bundles, having an oblique direction downwards and backwards over the upper surface of the hippocampus major, where they are separated from the tapetum (*CC tap*) by part of the choroid plexus, here stained yellowish-brown by WEIGERT's method.

The forceps major of the corpus callosum maintains the same position at the upper end of this part of the hippocampus major until we reach fig 12, when its fibres, which have hitherto been transversely or obliquely cut across, alter their direction. The whole mass is continued in a thick bundle in a direction downwards and backwards behind the upper end of the hippocampus major. These fibres, which are

deeply stained, cut right across the most external fibres of the cingulum (see p 146) as they lie between the hippocampus major and the calcarine fibres. When traced further some of these fibres of the forceps major seem to pass downwards behind the hippocampus major along with the descending fibres of the cingulum, but the majority of them course downwards and then turn sharply backwards into the white substance of the occipital lobe which is below the calcarine fissure, tapering as they proceed backwards. The course of these fibres is very decided, as they cut through the outer part of the descending cingulum, and they are best seen in fig 12 (*F.M*) where they form a very broad mass. Their ultimate ending cannot be definitely ascertained, but their direction is towards the cortex of the inferior and median parts of the occipital lobe below the calcarine fissure, a part which does not, as far as I have been able to ascertain, receive any fibres from the tapetum or from the main body of the corpus callosum, they certainly do not go towards the calcarine cortex.

At this level (fig 12) the tapetum can be traced backward to the most posterior part of the occipital lobe, where its fibres have a direction downwards and backwards.

In the next section the fibres of the forceps major have almost entirely disappeared, while, at the same time, the tapetum becomes enlarged. We have now reached a point which is external to the grey matter at the bottom of the calcarine fissure, and where the tapetum fills up the place occupied by this grey matter and by the forceps major. There is, therefore, the following arrangement. The corpus callosum at this level is represented by a considerable mass of fibres of an irregular quadrilateral shape, which is bounded above and below by the horizontal fibres of the corona radiata (posterior part). In front it is in contact with the posterior part of the caudate nucleus, as it is turning downwards and forwards; behind it is a space, probably the posterior cornu of the lateral ventricle, corresponding to the position of the grey matter at the bottom of the calcarine fissure, in front and below, the anterior margin of the corpus callosum forms the posterior wall of the lateral ventricle, which here separates it from the upper end of the hippocampus major. A prolongation of the corpus callosum is sent downwards and forwards behind the hippocampus major, but separated from it by the lateral ventricle, the direction of the fibres being downwards. The lateral ventricle is therefore an important landmark in this region, in distinguishing the corpus callosum from its forceps major. The position of the forceps major in relation to the lateral ventricle is always on its internal and inferior wall, while the tapetum is on the external and superior, according as the section is horizontal or sagittal. At the present level we can tell that the part of the corpus callosum now visible belongs to the main body from the fact that it is superior to the lateral ventricle. On the posterior and superior edge of the gyrus hippocampi there is a band of fibres whose direction is parallel to the tapetum, from which it is separated by the ventricle, probably these are fibres of the forceps major.

In the next section the corpus callosum has contracted to very small dimensions; the direction of its fibres is downwards and slightly forwards. It is seen as a horn-



shaped collection of fibres, surrounded on its upper and posterior sides by the horizontal fibres of the corona radiata or optic radiations. In front, the larger end of the horn abuts on the caudate nucleus, and below it, lies the lateral ventricle and the superior end of the hippocampal gyrus.

In the next section the caudate nucleus is prolonged downwards and forwards (forming the anterior wall of the descending cornu of the lateral ventricle) to join the small remaining part of the lenticular nucleus. At the upper end of the lateral ventricle, as seen in these sections, we have a small piece of the corpus callosum which has the same relation as before, but its fibres are directed more forwards. In the last section of this series extending as far out as the vertical level of the fissure of SYLVIVS, the basal ganglia are represented by a very small piece of grey matter, forming the anterior wall of the lateral ventricle.

The corpus callosum in its position at the upper end of the lateral ventricle is in contact with the basal ganglia in front (<sup>2</sup> caudate nucleus) and sends a prolongation backwards and downwards behind the hippocampal grey matter, with which, however, no connection can be made out. These fibres, which are really the remains of the tapetum, are still seen on the superior wall of the descending cornu of the lateral ventricle, and they form a crescent-shaped collection of fibres arching over the superior and posterior ends of the hippocampal grey matter. They have a direction forwards and downwards, but their ultimate ending cannot be ascertained in sagittal sections.

*Horizontal Sections* — The relation of the posterior part of the corpus callosum will now be described in horizontal sections, and here, as in the sagittal, we shall consider it under the heads of (1) the posterior part of the body of the corpus callosum, with its prolongation backwards, the tapetum, (2) the splenium, with its prolongation backwards known as the forceps major posterior, (3) an intermediate part connecting the splenium with the posterior part of the body of the corpus callosum.

As was seen in the sagittal sections, the great distinctive difference between the two parts of the corpus callosum is, that with the exception of the region near the middle line, they are separated by the lateral ventricle. The main body, with its tapetum, being external and superior to this cavity, whilst the splenium with its forceps major is inferior and internal.

The first definite appearance of the corpus callosum from above is seen (fig. 13, *CC*) outside the cingulum, and also in the occipital region. It here forms a small club-shaped collection of fibres, which is bounded on the outer side by the corona radiata, and on the inner side by the calcarine fibres (*Cf*). It is prolonged backwards in the form of a tail, forming a concavity towards the middle line, and the direction of the fibres is backwards and slightly inwards.

In the next sections (fig. 14), this arrangement of the corpus callosum is more marked, and the tail of the fibres above described is seen to be prolonged backward along the concave wall of a space (*Lvp*), which is evidently the commencement of the posterior cornu of the lateral ventricle. The direction of the fibres is now back-



wards and outwards. When traced forward, this part of the corpus callosum (*C.C. tap*) is found to be in connection with a tract of fibres which extends forwards along the whole length of the brain as far as the frontal region, and which is bounded on its inner and on its outer side by the cingulum (*Cing. h*), and the fibres of the corona radiata (*C.R.*), respectively. This tract is the main part of the corpus callosum (*C.C.*), whilst the club-shaped collection of fibres and its prolongation into the occipital region is the highest part of the tapetum (*Tap*).

In fig. 15 the corpus callosum is well seen in its whole length, extending from the frontal region into the posterior part of the occipital. We here have the first appearance of the caudate nucleus and the lateral ventricle, which is beginning to separate off the middle part of the corpus callosum from the centrum ovale.

It is not until we arrive at the level where the lateral ventricle is well exposed (fig. 16), that we perceive the first indication of that part of the corpus callosum (*Spl'*) which connects the splenium to the main part. In this section the posterior part of the body of the corpus callosum is well represented by a thick mass of fibres (*C.C.*), which have near the middle line a transverse horizontal direction, but which on passing outwards turn backwards, and are continued into the club-shaped bundle of fibres which can be traced sweeping round nearly to the tip of the white matter of the occipital region. These are the fibres which form the tapetum (fig. 16, *Tap.*) They are, as before, separated by a very narrow space, the posterior cornu of the lateral ventricle (*L.v.p.*), from the calcarine fibres and the cingulum (*C.f.*, *Cing. p*).

The posterior cornu (*L.v.p.*) is seen at its anterior part to separate off a tract of fibres from the main part of the corpus callosum. This tract (figs. 16-22, *Spl'*) appears on the inner side of the space as a collection of horizontal fibres, but towards the middle line it joins the rest of the corpus callosum. In an external and posterior direction its free border is bevelled off like a chisel, and its fibres are there cut horizontally across. This is the first appearance of the connecting fibres of the splenium in horizontal sections, and it is here bounded in front by the ventricle, behind by the fibres of the cingulum and their prolongation outwards.

On first examining these sections this tract of fibres (*Spl'*) appeared at first to be the splenium proper, but on a more careful comparison of these sections with those in the sagittal direction I think there is no doubt that this tract is that part of the corpus callosum which is intermediate between the posterior part of the body of the corpus callosum and its splenium.

The connections and relations of this tract are important; at first (fig. 16) its fibres can hardly be separated from the body of the corpus callosum, but in lower sections (fig. 22) the lateral ventricle has separated them at their outer part, and the direction of its fibres is different in the several levels.

Thus, above (fig. 16), nearly all the fibres are cut across, but, as we descend, the number of these diminish, and they are limited to the extreme posterior border of the tract, so that in fig. 20 the fibres have an oblique direction, which becomes more

horizontal as we reach fig 22, also in the upper section (fig 16) no continuity can be traced between the fibres of this tract and the middle line of the corpus callosum, but, as we descend (fig 22), the course of the most posterior fibres of the corpus callosum is horizontally outwards from the median line into this tract, and here, as has been already shown, the direction of the fibres is horizontal.

The appearance of the fibres being cut across in the upper sections, would show that they are either ascending or descending, and in the lower sections that they are oblique or horizontal. However, as we pass from upper to lower sections, the tract advances forwards, away from the occipital region, this would give the fibres a direction from above, downwards and forwards—the direction which this tract assumes in sagittal sections (fig 5, *Spl'*). Another point is that this tract is in close contact with the cingulum (fig 16, *Spl'*, *Cing p.*), whereas, in sagittal sections (fig 5, *Spl*), the splenium proper is separated from the cingulum by the isthmus of the gyrus fornicatus.

In the next section (fig 23, *Spl'*) the intermediate part of the corpus callosum ends abruptly at its outer end, while towards the middle line it blends with the posterior part of the body of the corpus callosum, which, as will presently be described, here becomes separated from its prolongation backwards—the tapetum. More inferiorly we get below the level of these two parts of the corpus callosum, and have only the splenium proper to deal with (fig 26).

In fig 23 we have reached the level where the tapetum (*Tap*) has become separated off from the posterior part of the corpus callosum, which here ends abruptly not far from the middle line, it now appears as a club-shaped collection of fibres, having the tail of the caudate nucleus (*cn*) in front, the mass of fibres of the centrum ovale on its outer side, and posteriorly it ends in a tail, which, tapering as it proceeds backwards, can be traced to the posterior part of the occipital lobe. This prolongation backwards is bounded the whole way by the fibres of the centrum ovale, which are almost at a right angle to the tapetal fibres, whose direction is downwards and outwards. There is certainly no communication between them. On the inner side of the tapetum, which is prolonged backwards behind the limit of the lateral ventricle, we have the calcarine fibres (*Cf*).

The club shaped part of the tapetum is bounded on its inner side by the lateral ventricle, which here contains the choroid plexus, separating it from the prolongation backwards of the splenium, viz, the forceps major.

The forceps major makes its appearance (fig 23, *FM*) as a band of fibres just outside the intermediate part of the corpus callosum (*Spl'*), but not in connection with it, and passes round in front of the commencing cornu Ammonis or hippocampus major (*C.A*), which here begins to form a projection forwards into the lateral ventricle. The fibres of the forceps major have a horizontal direction and end abruptly at their outer part, and posteriorly, where they are in contact with the cingulum, they are cut horizontally across.

In the next sections (fig 26) we have got below the level of the main part of the corpus callosum, and only the splenium is seen, extending from the middle line into its forceps major round to the outer side of the hippocampus major, but in the whole extent of this course no definite connection can be found between the fibres of the forceps major and the cortex of the cornu Ammonis.

In the above account the corpus callosum lies in close relation with the fornix, which appears in front of it. The two structures are separated at first by an interval, but they afterwards come into contact (fig 24); the difference in staining, as was observed in other sections, is well marked, especially in fig. 28, where the darker stained fibres next to the cornu Ammonis are the forceps major, and the light-coloured fibres next to the tænia hippocampi the fornix.

The horizontal fibres of the splenium and the forceps major gradually diminish as we descend, until we reach (fig 29, *Spl*) the apex of the wedge-shaped splenium (as seen in sagittal sections).

In the next sections this has disappeared, leaving only that part of the forceps major which is external and posterior to the hippocampus major, the fibres of which are cut across, and are arranged in a triangular-shaped bundle (figs 29-34, *F.M.*). Where the last traces of the forceps major in front of the cornu Ammonis are seen (fig 29, *Spl*), there are some faintly stained fibres, which, as we saw above, are part of the fornix. This is particularly seen in the next section (fig 30), where the light colour shows that they belong to the fornix (see p. 186).

In further sections we have then, representing the forceps major, the collection of cut-across fibres situated on the inner wall of the lateral ventricle, behind the cornu Ammonis. They are very deeply stained, and, at first sight, seem to be the continuation of the fornix round the ventricular surface of the hippocampus major. But in further sections, these fibres from the fornix, when traced to the posterior part of the cornu Ammonis, are quite distinct from the forceps major.

As has been seen in other planes, the two systems, viz, the splenium with its forceps major and the fornix with its alveus, lie so closely together that it is difficult to say where one begins and the other leaves off. This has been particularly seen in sagittal and frontal sections. In these horizontal sections, the prolongation of the forceps major round the outer side of the cornu Ammonis, and the prolongation of the alveus from the fimbria of the fornix lie one above the other. We have here reached a point where the two systems come in contact, and those fibres which, after winding round the cornu Ammonis, do not run into the triangular collection of fibres of the forceps major behind the cornu, but end in a separate collection in front of this triangle, are the first indication of the alveus (see p. 187).

As was stated above, the forceps major (fig 35, *F.M.*) lies on the inner wall of the lateral ventricle behind the cornu Ammonis, forming a triangle the apex of which is directed backwards. In front of it is the alveus (*Alv.*), and behind it the calcarine fibres (*C.f.*).

In the next sections (fig 36), these fibres of the forceps major, which have hitherto been cut across, *i e*, descending, become oblique and are prolonged backwards. We have here reached the bottom of the calcarine fissure (*FC*) where the calcarine fibres can be seen passing along its floor. Lower down (figs 37, 38) we have got almost below these fibres, and can now see those of the forceps major (*FM*) spreading out like a bush, and having a direction backwards and inwards. A few of the most inferior calcarine fibres can still be seen on the outer side of the forceps major, having a direction at right angles to its fibres, which they separate from the calcarine cortex. Further on, this appearance is better marked (fig 38, *Cf*). The calcarine fibres at the bottom of the fissure soon disappear altogether, and the forceps major has the following arrangement. Just behind the cornu Ammonis the fibres appear as points, *i e*, cut across, and from this place they radiate backwards, spreading outwards and inwards, and lose themselves in that part of the white matter of the occipital lobe which is derived from the posterior part of the corona radiata and the optic radiations of GRATIOLET.

Their ultimate ending in the cortex cannot be traced in these sections, but they certainly do not join the corona radiata, with whose fibres they make sharp angles.

Further on, we get below the level of the forceps major, which disappears gradually, and the space is filled up with the white matter of the corona radiata, whose fibres now turn sharply round to reach the cortex of the gyrus hippocampi, for now a section has been reached which is below the level of the posterior cornu of the lateral ventricle.

In sagittal sections it appeared as though the forceps major sent some fibres downwards into the temporo-sphenoidal lobe, but this point cannot be made out in these horizontal sections.

Having now described the forceps major in horizontal sections, the further course of the tapetum (the prolongation backwards of the main part of the corpus callosum) must now be followed out.

As already mentioned, it forms a club-shaped bundle of fibres on the outer wall of the posterior cornu of the lateral ventricle. This shape gradually becomes more triangular, diminishing in size, it at length (figs 35-38, *Tap*) forms a narrow band lying immediately behind the tail of the caudate nucleus (*cn*), and extending to the hindermost part of the posterior cornu. The direction of its fibres has also altered, and they are now cut across (*i e*, descending), standing out as points in marked contrast to the fibres of the corona radiata, which are horizontal. This arrangement is seen as far as the end of the posterior cornu, where the fibres of the tapetum again become more horizontal.

In further sections the tapetum can be traced to the level where the posterior cornu leaves off and the descending cornu of the lateral ventricle begins. On the outer wall of this cavity the tapetum is again seen immediately behind the caudate nucleus as a very thin band, its fibres having a direction at first backwards and inwards and then downwards. Its further appearance is in the form of small dots and in the same

position, as far as the section corresponding to the horizontal level of the optic commissure, after which it can no longer be made out. It will be seen by the very small size of the tapetum that its distribution in the descending cornu must be very slight.

*Frontal Sections* — The first appearance of the splenium of the corpus callosum is seen in frontal sections at the vertical level through the middle of the pons and the posterior part of the optic thalamus. It there appears as a narrow band of fibres having a transverse direction and separated by a horizontal septum from the under surface of the main part or body of the corpus callosum, at the outer part of this septum, the longitudinal fibres of the fornix are seen.

Passing posteriorly to the next section, which is made at the vertical level where the optic thalami are completely separated from the hemispheres, the splenium is much larger, and it soon becomes the same thickness as the main part of the corpus callosum.

At the outer and upper part of the splenium is the fornix, separating it from its main body. The fibres of the splenium end abruptly at the outer margin, and their direction is obliquely transverse, they are also rather deeply stained. On the other hand the fibres of the fornix are quite distinct from those of the splenium, being more closely aggregated and only faintly stained.

As mentioned above, there is a distinct septum running transversely, separating the two parts of the corpus callosum, and along it the fornix extends only for a short distance, so that at the median line the splenium is in such close contact with the under surface of the body of the corpus callosum that the two cannot be differentiated.

In the fronto-oblique sections the splenium is not definitely seen until we reach that made through the corpora quadrigemina (fig 43, right half, *Spl.*) Here the corpus callosum is much enlarged in its vertical direction, and at its outer margin is the fornix (*F. p.*), very faintly stained. Winding round the outer surface of the cornu Ammonis, which is here very much enlarged, there is a narrow band of fibres more darkly stained than the fornix, with which it comes in close contact in the lateral ventricle. These darker stained fibres can be traced down to the under surface of the gyrus hippocampi, and they are probably the commencement of the forceps posterior of the splenium. It is here very difficult to demonstrate, for certain, where the descending posterior pillar of the fornix (*tænia hippocampi*, *alveus*) leaves off, and where the forceps major of the splenium begins, for both of them wind round the outer surface of the cornu Ammonis along the inner wall of the lateral ventricle, to end in the white substance of the temporo-sphenoidal lobe.

It is seen, however, that whereas the forceps major can be traced inwards in this plane into the most inferior part of the corpus callosum, *i.e.*, the splenium, the posterior pillar of the fornix appears to spring from the septum between the two parts of the corpus callosum. Moreover the former is more deeply stained than the fornix, and it does not present the sharp angle which the latter makes at this level.

In the sagittal and horizontal sections the same difficulty was experienced in differentiating the two systems, but in the fronto-oblique sections the arrangement can be more clearly seen. As we pass backwards the forceps major gradually increases in size, while the posterior pillar of the fornix diminishes and finally disappears, showing that the fornix lies in part of the forceps major. At the succeeding fronto-oblique levels (fig 45, right), the splenium (*Spl*) appears as a projection outwards on the under surface of the corpus callosum, its fibres being cut across obliquely. At its outer end it is connected with the forceps major (*FM*), which extends as a thick band along the outer side of the fascia dentata (*FD*), forming the inner wall of the lateral ventricle. This is better seen (fig 41, left) where the forceps major (*FM*) passes outwards, downwards, and backwards to the level of the floor of the lateral ventricle, where it forms a thick collection of fibres between the cingulum (*Cing p*) on the inside, and the lateral ventricle (*Lvp*) on the outside. The forceps major is separated by a slight space from the fascia dentata and cornu Ammonis, and no fibres can be traced from it into their cortex. At the level of the floor of the lateral ventricle the fibres end abruptly.

In the next sections (fig 42, 43, left) the outer wall of the lateral ventricle, which in the previous sections was formed in part by the tail of the caudate nucleus (fig 41, left, *cn*), is now made up entirely by the tapetum of the corpus callosum. The tapetum is seen (fig. 41, left, *Tap*) in all sections anterior to this (as far forwards as the anterior part of the descending cornu), as a narrow band of fibres extending downwards from the lower margin of the caudate nucleus to the level of the floor of the lateral ventricle (descending cornu). On passing backwards this part of the tapetum increases in length at the expense of the caudate nucleus, until at the posterior limit of this nucleus, the tapetum (fig 44, left, *Tap*) extends along the whole outer wall of the lateral ventricle, springing out of the main body of the corpus callosum above, and tapering gradually downwards to the level of the floor of the lateral ventricle below, where it comes into contact with the forceps major.

From the outer surface of the posterior part of the corpus callosum fibres are sent to pass through the whole matter of the centrum ovale. The plane of the fibres is downwards and backwards, and at right angles to those of the centrum ovale, which here have a sagittal direction. At this point, therefore (fig 44, left), the posterior cornu is lined entirely by the prolongations from the corpus callosum, having the forceps major on its inner, and the tapetum on its outer wall. Both these parts increase very much in size, and the forceps major at its lowest part forms a large collection of fibres, ending abruptly below the calcarine fissure on the inner side of the floor of the lateral ventricle. This corresponds to the point in horizontal sections where the forceps major radiates backwards in a horizontal plane (see p. 175).

In the next section (fig 45, left) the forceps major gradually disappears when traced down the inner wall of the lateral ventricle.

It should, however, be remarked that there is still a collection of fibres in the



central white matter of the convolution forming the lower lip of the calcarine fissure in the place occupied by the termination of the forceps major, and it is, moreover, situated near the inferior end of the tapetum (fig. 44, left, *F.M.*) These fibres are therefore the last part of the forceps major, they have a direction downwards and inwards and are in contact above with the calcarine fibres (*Cf.*), which separates them from the calcarine cortex.

Here (fig. 45, left), although the fibres of the forceps major diminish in extent and thickness, there is still a collection of fibres at the point where the forceps major leaves the corpus callosum (fig. 44, left, *Spl.*) which does not become smaller or less deeply stained. This collection of fibres is oblong in shape and is situated at the upper end of the lateral ventricle, it is attached above to the main part of the corpus callosum, and its long axis slants downwards and outwards to its lower end which is bevelled off, on its inner side it rests on the grey matter of the isthmus of the gyrus fornicatus—a faint trace of the fascia dentata being also visible—and on the outer side it is separated by the lateral ventricle from the tapetum. The direction of the fibres which was previously down and out, now alters; they become more and more oblique, till they appear as bundles of points, showing that they are cut across and are now taking an antero-posterior direction. Before this condition is reached the upper part of the forceps major has entirely disappeared. These fibres, when traced backwards, do not vary their position, but keep to the inner side of the upper end of the lateral ventricle—the angle which they make with the tapetum forming the roof of this cavity. This tract alters in shape, becoming more triangular, and has the same relations, except that it is now (*i.e.*, posterior to fig. 45) bounded by the cingulum on its inner and under surface. Its fibres can be traced to the end of the posterior cornu of the lateral ventricle, and after that they blend with the tapetum. As to what is the distribution of this part of the corpus callosum it is difficult to be certain; it is very doubtful if it gives off fibres to the subjacent cortex, but in this plane the connection cannot be definitely made out.

I think there is no doubt that these are the fibres which come from the intermediate part of the corpus callosum, which is situated between the posterior part of the body and the splenium, and which was seen in sagittal (fig. 5, *Spl.*) and in horizontal sections (fig. 22, *Spl.*) forming along with the tapetum the superior and inner angle of the posterior cornu of the lateral ventricle. In horizontal sections the shape of this tract with the bevelled edge is very similar to the appearance in the fronto-oblique sections.

The tapetum can be traced (in sections posterior to fig. 45) to below the level of the floor of the lateral ventricle and that of the calcarine fissure, where its fibres end in the mass of white matter of the hemisphere. Although the individual fibres cannot be traced into the cortex, their direction makes it probable that the tapetum sends fibres to the outer part of the occipital region, whilst the forceps major supplies the cortex on the median and inferior surface of the occipital lobe below the level of the calcarine fissure.



In following the corpus callosum further backwards we arrive at the end of the posterior cornu of the lateral ventricle, which is diminished to a very small size. It is bounded on the outer side by the tapetum of the corpus callosum, which extends downwards to the under part of the occipital lobe, and on the inner side by the fibres from the intermediate part of the corpus callosum, which presents a small collection of cut-across fibres.

In the next section, which is behind the posterior limit of the lateral ventricle, these two parts of the corpus callosum come into contact, and, in the last section, it is almost impossible to separate them.

*Summary* — From the foregoing description of the hinder part of the corpus callosum and its splenium in the various planes, we see the following arrangement — At the middle line, and for a short distance on either side, these two parts of the corpus callosum are so closely united that it is almost impossible to separate them, although under the microscope a narrow septum can be traced transversely between them. Outside this level (fig 6), the two begin to be separated by the lateral ventricle. The main part or body of the corpus callosum ends posteriorly on either side in the tapetum, which runs backwards and outwards along the roof and outer side of the posterior cornu of the lateral ventricle. It also extends along the outer wall of the descending cornu of this cavity as far forwards as its anterior part. The anterior margin of the tapetum is formed by the tail of the caudate nucleus, lying behind which it is always seen in horizontal and sagittal sections. The tapetum is therefore distributed to the parts of the hemisphere bounding the posterior and inferior cornua of the lateral ventricle on their outer side, though, to judge from the size of the tapetum in the anterior part of the descending cornu, its connection there must be very slight.

The splenium, which is at first oval on sagittal section at the middle line, becomes triangular as it extends outwards, and more separated from the main part of the body, and connecting these two is the intermediate part of the corpus callosum, which is continued backwards between them into the occipital region. The splenium is now prolonged, as the forceps major posterior, obliquely downwards and backwards round the anterior and external surfaces of the cornu Ammonis, or hippocampus major, to the posterior inferior aspect of that structure (*FM*, figs 11, 23). In this course it forms the inner wall of the posterior cornu of the lateral ventricle, but as far as can be made out it does not seem to send any fibres into the hippocampus major. The forceps major has now been traced down to the floor of the lateral ventricle and below the level of the calcarine fissure, where it (*FM*, figs 12, 38, 41) turns sharply backwards at an obtuse angle, and spreading out it passes into the mass of fibres coming from the corona radiata. Its shape thus resembles the letter **Z**, if its acute angles be made obtuse.

Though its individual fibres cannot be traced into grey matter, its direction is towards the cortex on the inferior and median part of the occipital lobe below the

level of the calcarine fissure, and it apparently does not supply the calcarine cortex. The terminal fibres (*FM*, fig 38), which course in the direction of the hinder end of the posterior horn of the lateral ventricle, come into contact there with the tapetal fibres.

The intermediate fibres (*Spl'*, fig 4), between the tapetum and the splenium proper, run backwards, being attached at their upper and inner end to the tapetum, but soon become free of the splenium and forceps major (*Spl'*, figs 5, 22). After passing the vertical level of the forceps major, the fibres can be traced along the roof of the posterior cornu of the lateral ventricle, forming with the tapetum the apex of the upper part of this cavity (fig 45, left), here they may give off fibres to the cortex of the gyrus fornicatus, but not to that forming the upper lip of the calcarine fissure, and they can be followed posterior to the lateral ventricle, where they blend with the tapetum.

From the above description it appears that the arrangement of the different parts most resembles the account given by SCHWALBE (p 165), and especially with reference to the opinion that the upper and posterior parts of the occipital convolutions are supplied by the callosal fibres coming from the angle formed by the splenium with the body, and which I have here termed the intermediate fibres. The relation of this part to the tapetum, and the manner in which the two parts together form the roof of the lateral ventricle has not, I believe, been fully described. I have been unable to trace any fibres from any part of the corpus callosum to the cortex bounding the calcarine fissure.\*

I would again emphasize the relation of the callosal fibres to the corona radiata; in no case has any junction been found between the terminal fibres of these two great systems, a connection which has been so strongly insisted on by Professor HAMILTON, and which I have already contested in a previous paper (see 'Bram,' Parts XXXI., XXXIII.) with regard to the other parts of the corpus callosum.

In the last part of this paper will be described the fornix, and particularly the body and the posterior crura.

### *Posterior Part of the Fornix*

*Previous Descriptions*—It is stated in QUAIN'S 'Anatomy'† that each anterior pillar of the fornix is connected near the foramen of MONRO with the peduncle of the pineal gland and with the tænia semicircularis, and it also receives fibres from the septum lucidum.

\* [The calcarine cortex corresponds to the cuneus in Man and the higher Apes, which is considered by some to be the chief localisation for the opposite half of the visual field. The possible absence of a commissure between the two sides might explain the persistent hemiopia after lesion of the cuneus in Man—February 24, 1891.]

† *Loc. cit*, p. 348.

"The posterior pillars, or crura, of the fornix are the diverging posterior prolongations of two flat lateral bands composing the body. Each crus enters the descending cornu of the lateral ventricle, where part of its fibres are distributed on the great hippocampus, and the remainder are prolonged as the narrow band of white matter known as the *tænia hippocampi* or *fimbria*."

In the same work\* the *tænia semicircularis*, or *stria terminalis*, is described as "a narrow whitish band between the nucleus caudatus and the optic thalamus. It forms part of the floor of the lateral ventricle, and it is continued backwards into the white substance of the roof of the descending cornu, and finally ends in the nucleus amygdalæ in the inferior cornu. In front, where it is largest, it reaches the corresponding anterior pillar of the fornix, with which it comes into connection."

According to MEYNERT† the crura fornicis possess a commissure below the splenium of the corpus callosum and within the psalterium. According to the same author and HUGUENIN, the crura fornicis are augmented by fibres from the medullary lamina of the cingulum at the anterior part, where they form the body of the fornix, these fibres pass through the corpus callosum transversely, and join the fornix.

HUGUENIN‡ states that the "fibres of the alveus proceed from the cortex of the cornu Ammonis, but they ascend to the trigonum in the posterior pillar of the fornix, which higher up sends some of its fibres to the opposite side through the psalterium, so that there exists between the two cornua Ammonis a transverse commissure. Directly after the junction of the posterior pillars with each other, along the median line, they receive a new band of fibres which, proceeding from the association fibres of the cingulum, pass through the fibres of the corpus callosum, unite with the trigonum, and accompany the latter in its course, and descend in front of the anterior commissure."

OBERSTEINER,§ after giving the relations of the fornix according to the description already given, says that "the two posterior crura of the fornix enclose on the under surface of the corpus callosum a triangular area, with clearly-marked transverse arrangement of fibres, and with the apex of the triangle directed forwards (*psalterium lyra Davidis*). It consists of a thin medullated layer, which is often incompletely united with the under surface of the corpus callosum, but which is separated from it by a cleft (the ventricle of VERGA)."

Further on in his work,|| he says that "there is no doubt the fornix contains many fibres which, coming out of the cortex of the Ammon's horn, seem to end in the corpus mamillare, and therefore are analogous to the fibres of the corona radiata. A small part of the fibres of the fornix, which radiate into the septum lucidum, must be

\* P 352

† *Loc cit*, p 760.

‡ *Loc. cit*, p 134

§ *Loc cit*, p 69.

|| *Loc cit*, p 343

reckoned as association fibres, as the septum is to be looked upon as part of the cortex cerebri ”

The part of the fornix with which we are concerned in this paper, is the highest part of the arch, which lies in the floor of the lateral ventricle on the optic thalamus, and is commonly called the body of the fornix, as well as the posterior part of the arch, which descends the inferior cornu of the lateral ventricle

It may be said at once that the anterior part of the fornix known as the ascending and descending pillars, will not form part of this paper, as the subject has already been worked out by VON GUDDEN and FOREL (‘Archiv f Psychiatrie,’ vol 7, p 77, vol 7, p 422, vol 11, p 428).

*Sagittal sections* —The horizontal fibres which form the highest part of the arch of the fornix are seen in the lateral ventricle, lying beneath the corpus callosum, and resting on the optic thalamus in the groove between this body and the caudate nucleus (fig. 1, *F*)

Its fibres, which have an antero-posterior direction, can be traced backwards to the splenium of the corpus callosum. In this course, just before they reach the splenium, the fibres are doubled back upon themselves, so as to form a sigmoid appearance, which, as we proceed outwards from the middle line, becomes more posterior, until at last it reaches the splenium.

On arriving there its fibres are divided into two parts by the splenium —(1) Some of them pass above it and enter into the posterior part of the corpus callosum, where they have a direction at right angles to its transversely cut fibres, and thus separate off the splenium from the main body of the corpus callosum; (2) In sections further removed from the middle line, the rest of the horizontal part of the fornix passes down in front of the splenium, between it and the posterior border of the optic thalamus. This, as will subsequently be seen, is the commencement of the part called *tænia hippocampi*, which descends the inferior cornu of the lateral ventricle to reach the cornu Ammonis, where it is also known as the *fimbria*.

To return to the fibres of the fornix which pass above the splenium. As stated above, they pass into the corpus callosum. They appear (figs. 1-4, *F.m.*) as a very fine bundle connected with the body of the fornix in front, and behind they pass into the septum between the splenium of the corpus callosum and its main part. The fibres there take a direction upwards and backwards, at right angles to that of the fibres of the corpus callosum. The individual fibres of the fornix can be traced as far as the superior surface of the posterior part of this structure, but what their final ending may be, cannot be ascertained. They appear as septa between the thick bundles of the corpus callosum, but whether they pass out with its fibres to join grey matter elsewhere cannot be here made out. They do not seem to be continuous with the cingulum as has been described by HUGUENIN.

The other part of the fornix, lying in front of the splenium and behind the optic thalamus, must now be described.

The first appearance of the fibres of the horizontal part of the fornix descending in front of the wedge-shaped splenium of the corpus callosum is in fig 5 (*Fl*)

Here the bundles of the transverse fibres of the splenium (*Spl*) are seen, and in front of them is a narrow band of fibres from the body of the fornix descending to the apex of the splenium, where they become more or less transverse in direction. They continue to pass down along the descending cornu of the lateral ventricle, being bounded in front by the pulvinar of the optic thalamus, and behind by the commencing fascia dentata of the gyrus hippocampi. During this time the transverse fibres of the splenium alter in shape, and are readily distinguished from the descending fibres of the fornix by their marked transversely-cut appearance, and by the fact that they are more deeply stained (by WEIGERT's method) (fig 10, *FM*, and *Fl*).

The posterior pillar of the fornix continues descending, and finally joins the fimbria of the cornu Ammonis (fig 11, *Fimb*), the fibres still preserving their peculiarity of being stained a lighter colour (by WEIGERT's method) than the adjacent fibres of the splenium.

At a point half way down the descending cornu the fimbria (fig. 11, *Fimb*) appears to form a fusiform enlargement lying behind the lower part of the corpus geniculatum externum (*cge*). The part of the fimbria beyond this enlargement is very narrow, where it is known as the alveus (*Alv*), while the part above this becomes much increased so as to be the same size throughout (fig 12, *Fimb*.) \*

The fibres of the tænia hippocampi have a distinctly longitudinal direction and are exactly parallel to the posterior curved surface of the corpus geniculatum externum, from which it is separated by the descending cornu of the lateral ventricle.

The tænia hippocampi, or the fimbria, is prolonged downwards along the whole extent of the free margin of the fascia dentata of the gyrus hippocampi to the lower end of the ventricle, and then over the extreme anterior end of the cornu Ammonis, when it is known as the alveus (figs. 11, 12, *Alv*), and it here separates this gyrus from the hippocampal or pyriform lobule (*H.L*) with the nucleus amygdalæ.

The relation of the tænia to the cortex of the hippocampal convolution must now be described, beginning with the lowest part.

In the sections of this series, nearest to the middle line in which the inferior part of the cornu Ammonis first appears (fig 5), the lowest end of the alveus is seen bounding the anterior and superior surfaces of the cornu Ammonis (*CA*), but separated by a space from the hippocampal lobule in front of it. On microscopical examination the alveus has no connection with the hippocampal lobule, and this statement holds good throughout this series of sections.

\* [The tænia hippocampi, or fimbria, is the continuation of the crus posterius fornicis and forms a thick band of fibres on the superior and anterior surface of the fascia dentata, whereas the alveus denotes the narrow band of fibres proceeding from the fimbria round the anterior and external surfaces of the cornu Ammonis to its inferior and posterior surfaces —February 20th, 1891.]

This lowest end of the alveus (figs. 8-10, *Alv*) can be traced into a leash of fibres which turn downwards and spread out across the cingulum (*Cing.*, *p*), to end in the cell layer of the cortex on the inferior surface of the temporo-sphenoidal lobe. This leash of fibres in which the alveus ends, is in close contact with that formed between the termination of the cingulum and the superficial fibres of the gyrus hippocampi, but even with high powers (F, ZEISS) no definite connection can be made out between the two.

The alveus (fig. 10, *Alv*) has here a direction parallel to the superior and anterior surface of the cornu Ammonis, and when traced upwards, appears to give off fibres into its cell layer. It appears to do so because, although numerous fibres are seen in the adjacent layers of the cortex, there is not that extensive radiating out of fibres from the alveus which is seen in other parts.

At the upper surface of the cornu Ammonis the fimbria (fig. 10, *Fimb*) sends down fibres into its cortex, and in some sections the plexus is continued downwards into the central part of the grey matter of the fascia dentata (*F. D*).

On looking at the next section (fig. 12), where the fimbria (*Fimb.*) and the alveus form a continuous band reaching from the upper part of the hippocampus major and the tail of the caudate nucleus (*Alv*, *c.n.*, fig. 11) to the anterior inferior end of the cornu Ammonis below, it can be made out that along the whole of this course where the fimbria is in contact with the grey cortex of the cornu Ammonis, a fine plexus is given off into it.

It is difficult to say for certain in which direction the fibres are given off from the part of the fimbria which is parallel to the surface, but in the alveus it is still from the cortex of the cornu Ammonis, downwards and forwards, in fibres of short lengths. It will be observed on looking at fig. 12 that the convoluted appearance of the fascia dentata (*F.D.*, fig. 11) gradually disappears, and at the same time the outer cell layer of the cornu Ammonis extends upwards at the expense of the fascia dentata. Into this extension of the cell layers of the cornu Ammonis, fibres are sent off by the tænia. The direction of its fibres at the upper part is now probably downwards and forwards into the cortex. At the same time the lower end of the alveus (fig. 12, *Alv.*) begins to extend round the inferior surface of the cornu Ammonis, so as to separate this from the underlying cingulum (*Cing p.*) The direction of the fibres of the alveus is a transverse one, *i.e.*, the fibres appear in section as points, and in marked contrast to the longitudinal fibres of the cingulum.

These fibres of the fimbria in succeeding sections gradually appear further backward along the inferior surface of the cornu Ammonis, while, at the same time, the tænia hippocampi or fimbria gradually loses its upper end (*i.e.*, the part between the tail of the caudate nucleus and the optic thalamus). In further sections outwards the fimbria diminishes still more, until the cornu Ammonis, as here seen, is completely surrounded by only a thin band of fibres, which must be the alveus, as the section is now external to the level of the fimbria (see fig. 38). This appearance becomes more



marked on passing outwards, and in the most external sections of this series the cornu Ammonis is seen as an oblong piece of grey matter encircled by a band of fibres which are arranged in short cut bundles and completely separate this gyrus from the surrounding structures, viz —at the upper and posterior end, the remains of the corpus callosum, in front, the descending cornu of the lateral ventricle and the descending tail of the caudate nucleus, which here joins the outermost part of the lenticular nucleus, further in front are the remains of the nucleus amygdalæ and inferiorly the fibres from the posterior part of the internal capsule, which are visible as far forward as this nucleus

The direction of the fibres surrounding this, the extreme outer part of the cornu Ammonis, is important. The level now reached is so external that these fibres must be looked upon as part of the alveus (*cf.* horizontal sections, fig 38), except at the extreme upper end where they may form part of the fimbria. On the upper surface, which is bounded by the descending cornu of the lateral ventricle, the fibres are in short-cut lengths and are directed forwards and downwards *towards* the cortex, but they do not give off many fibres. At the lowest anterior end of the lateral ventricle they become parallel to the surface of the cortex, and round the front of the cornu Ammonis they change their direction and go downwards and forwards *from* the cortex. As the under surface is reached the direction of the fibres is confused and becomes at right angles to the cortex, and for the rest of the distance from here to the upper end of the lateral ventricle the fibres are in short lengths in the direction *from* the cortex down and forwards.

*Horizontal Sections* —The first appearance of the body of the fornix is seen in horizontal sections, when the level is reached where the lateral ventricle is first opened (fig. 16, *F*)

It there appears in the lateral ventricle on the inner side of and parallel to the inner border of the caudate nucleus (*CN*), and bounded on its inner side by the cut-across ends of the transverse fibres of the corpus callosum.

The direction of its fibres is backwards and outwards. The fornix increases in size as we proceed downwards and has in these sections a fusiform shape.

It lies free in the cavity of the ventricle, and at this level has no connection with the surrounding parts. It is bounded on the outer side by the choroid plexus, which separates it from the caudate nucleus. As we descend, a mass of grey matter (stained orange in the sections) appears in the middle of the fusiform shape of the fornix; this is the optic thalamus, which gradually separates the fibres of the fornix (figs 20–22, *OT*), but they are joined again behind that body, on the inner side the fibres soon disappear leaving the thalamus free. This appearance is explained by examining a frontal section (fig. 40) where the fornix rests on the thalamus like a roof, horizontal sections of which would expose the thalamus with the fornix on either side of it.

The fibres on the outer side of the optic thalamus, when traced forwards, end in a



small piece of grey matter occupying a median position and bounding the inner side of the lateral ventricle (figs. 22, 23, *S.L*) This is the septum lucidum.

We need not pursue these fibres any further forwards as it is outside the scope of the present work, and the termination of the anterior pillars of the fornix has already been worked out by Professors GUDDEN and FOREL

Posteriorly these fibres run between the optic thalamus and caudate nucleus to the hinder part of the former (fig 23, *Fl*), where they form a knob-like shape, which is situated in a cavity of the lateral ventricle, bounded on the inner side by the optic thalamus (*OT*), by the tail of the caudate nucleus (*c.n*) and choroid plexus on its outer side; and in front, by the medullated fibres of the corona radiata This part of the fornix, lying external to the optic thalamus, is gradually lost as we proceed to lower sections, and the two ends of the arch alone remain, viz., the anterior end in the septum lucidum (fig. 29, *S.l.*), which is now separated from the optic thalamus by the foramen of MONRO (*For M.*), and the posterior which forms the knob-like projection just referred to (*Fl*). This latter, as will be seen later on, is really the tænia hippocampi and its fibres soon assume a downward direction, i.e., they appear as if cut across (fig. 29, *Fl.*).

We must now return to the fibres of the fornix on the inner side of the optic thalamus.

In fig. 22 (*Fl*) these fibres have a direction backwards and outwards behind the optic thalamus, and lying just in front of the posterior part of the body of the corpus callosum, from which, however, they are distinctly separated, being stained by hæmatoxylin of a lighter colour

They are at first (fig. 23) free in the lateral ventricle, but in the next section (fig. 24) they come into close contact with the forceps major. In lower sections (fig. 26) the fornix appears as a thin faintly-stained band of transverse fibres, running outwards with the forceps major, but when traced inwards they do not extend to the middle line except in fig. 28. These are probably the transverse fibres which are considered to extend across the middle line to the other hemisphere, and to have a different course from those described above as lying internal to the optic thalamus. When traced outwards they join the base of the knob-like projection of the outer fibres of the fornix above referred to, and beyond this they pass into the cortex of the cornu Ammonis

It is exceedingly difficult to separate the course of these fibres of the fornix from those of the corpus callosum, but one is helped by the fact that the latter are stained by WEIGERT'S method a deep blue, almost black colour, while the fibres of the fornix are stained a lighter tint (see corpus callosum, p 174).

In fig. 29 (*Fl.*) the knob-like projection of the external fibres of the fornix, which we may now call the tænia hippocampi, or fimbria, is still seen to be descending, and to have the same relations in the lateral ventricle to the surrounding parts as before. At the base of the projection we have the light-coloured fibres of the transverse part

of the fornix, and behind them the transverse fibres of the forceps major of the corpus callosum

At fig 30, these fibres of the forceps major in front of the cornu disappear, leaving the transverse fibres of the fornix, which gradually diminish till we reach fig 32, where they disappear almost entirely, leaving the knob-like projection of the tænia hippocampi, which now lies quite free in the descending cornu of the lateral ventricle, except at its posterior part, where it rests on the cornu Ammonis, having the tail of the caudate nucleus on its outer and the optic thalamus on its anterior and inner sides, with the ventricle intervening. In figs 35-37, although there are no horizontal fibres of the corpus callosum or fornix on the inner side of the tænia hippocampi, there is a considerable band of fibres going out from the posterior part of the tænia, and running round the external surface of the cornu Ammonis to its hinder surface (*Alv*). These fibres appear as if cut into short lengths, having a direction from the cortex backwards and outwards. In this course they form the anterior part of the inner wall of the posterior cornu of the lateral ventricle, and wind round to the posterior surface of the cornu Ammonis. Posterior to this convolution and between it and the hippocampal gyrus, there is a considerable projection of white matter. At the outer part, next to the ventricle, three sets of fibres are to be recognised under the microscope—1st, the fibres of the fornix just described, coming round the outer surface of the cornu Ammonis from the tænia hippocampi, 2nd, the calcarine fibres (*Cf*) at the extreme posterior part, and 3rd, between the two a wedge-shaped mass of fibres, the forceps major (*FM*), having its outer surface free towards the lateral ventricle.

The differentiation of these fibres into three parts is better seen in sections stained by WEIGERT's method than by PAL's.

Besides these three sets of fibres, we must not forget the cingulum, which forms the most internal part of this portion of white matter.

The first of the three sets of fibres described above, which is considered to come from the tænia hippocampi or fimbria, forms what is known as the alveus of the cornu Ammonis, and its fibres can be traced on their inner side into its cell-layer, whence they pass in a direction outwards and backwards, while posteriorly, on arriving behind the cornu Ammonis, the direction of their fibres is evidently descending, and they finally blend with the fibres of the cingulum.

The alveus occupies the same place as the forceps major higher up, but whereas the fibres of the latter can be traced directly from the splenium, the former is narrower, and its individual fibres do not sweep round out of the fimbria, but they exist only in short lengths, instead of in one continuous band of fibres.

It will thus be seen that at this level the alveus lines the inner wall of the lateral ventricle which corresponds to the cornu Ammonis. On the other hand the whole outer wall of the posterior cornu is formed by the tapetum of the corpus callosum (*Tap.*)

The relation of the alveus to the cornu Ammonis and to the cingulum remains the same as far as fig 38 (*Alv*)

When traced further down still, we come to the level where the forceps major fibres cease, and where the posterior cornu of the lateral ventricle does not extend further back than the posterior surface of the cornu Ammonis, and the fibres from the posterior part of the internal capsule are turning sharply inwards to end in the hippocampal convolution. Here the knob-shaped fimbria, with its fibres cut across transversely, is well seen, as well as the alveus, proceeding from its outer border and occupying a position round the outer surface of the cornu Ammonis, behind which it comes into relation with the cut-across fibres of the cingulum

The part of the alveus nearest the fimbria shows short cut fibres arranged at right angles to the cortex of the cornu Ammonis, more posteriorly they pass from the cortex back and out, while near the cingulum the fibres appear as points.

In the section where we have nearly reached the level of the lowest part of the occipital cortex, the fimbria alters in shape. It becomes triangular, with the apex backwards, and its fibres are seen to be arranged in a distinctly antero-posterior direction. This direction is continued into the alveus for the first part of its course, where the fibres are arranged in short lengths at right angles to the cortex, but posteriorly near the cingulum the fibres appear as points on the convexity of the cornu Ammonis, *i.e.*, the part turned towards the ventricle; but on approaching the cingulum the fibres are cut obliquely, but for the most part run forwards and backwards. Where the fimbria and alveus are in contact with the cornu Ammonis they send a plexus into its cortex. This is especially the case at the anterior and posterior parts.

In the section which is on a level with the under surface of the frontal lobe, the last vestige of which is seen, the cornu Ammonis increases very much in size, owing to the fact that it is here cut across in a slanting direction as it descends forwards.

The fimbria is much increased in size, and it is turned inwards towards the crus cerebri, which lies on its inner side, whilst in front is the posterior cut end of the optic tract. Its most internal fibres are directed backwards and outwards, forming a thick plexus in the cornu Ammonis, while the rest of them have an antero-posterior arrangement. The relation of the alveus remains the same as before. When traced downwards the fimbria remains enlarged, with all its fibres directed inwards and forwards until we reach the level of the middle of the optic chiasma, after which the cornu Ammonis appears enormously enlarged, and then the fimbria suddenly diminishes, so that in the last section of this series the alveus takes its place and appears as points, separating the cornu from the hippocampal lobule, as the level is now below that of the fimbria.

*Frontal and Fronto-oblique Sections.*—Having discussed the fornix in sagittal and horizontal sections, it will now be examined in the frontal and in frontal-oblique planes. It will be more convenient to take the latter first, as they show the fornix

at a point further forward than in the frontal sections. In the most anterior sections, passing through the most anterior part of the pons and crus cerebri, the septum lucidum is well seen at the middle line, forming an irregular four-sided figure, being in contact with the under surface of the corpus callosum above, and bounded on the outer side by the lateral ventricle and below by the space known as the foramen of MONRO.

It contains some cut-across fibres, which gradually form a projection on its outer side. This increases at the expense of its grey matter, which gradually alters in shape, until we have the septum lucidum appearing as a narrow triangular piece of grey matter, and, attached to it below, a horizontal collection of fibres, which at the middle line are cut away, while at their outer part they become oblique. This is the commencing body of the fornix, which now comes into contact with the under surface of the corpus callosum, the choroid plexus intervening.

At the most inferior part of the septum lucidum there are a few transverse fibres which leave off abruptly at the middle line. Their nature is not known.

The fornix continues to increase outwards, the fibres there having an oblique transverse direction, whilst at the middle line there is a considerable collection of fibres which are cut transversely and have a longitudinal direction, and the grey matter of the septum lucidum is very slightly represented. We already see that the fornix here consists of two distinct parts: 1st, a median, 2nd, a lateral oblique. These correspond to the two divisions of the fornix seen in sagittal sections (p. 182). The median fibres appear as points, *i.e.*, they have a sagittal direction, whilst the lateral fibres are cut across obliquely.

The under surface of the fornix is now in contact with the superior surface of the optic thalamus, and so closes up the space leading from the lateral ventricle inwards between the fornix and the optic thalamus, this space or channel is known as the foramen of MONRO.

In the next section the fornix is closely applied along the whole of its under surface to the upper surface of the optic thalamus. At the inner part the small triangular piece of the septum lucidum still remaining begins to be separated off together with the median fibres of the fornix from the rest of the fornix by a space. Separated from this and lying closely applied to the corpus callosum above and on the optic thalamus beneath is the rest of the fornix presenting a number of obliquely cut fibres.

The fornix has now been traced to the fronto-oblique level of the posterior extremity of the lenticular nucleus and to about the middle of the pons.

Having now described the fornix so far in fronto-oblique sections, it will be convenient to examine it in frontal sections.

In the first frontal section, which is made at the vertical level of the optic commissure (fig. 39), the fornix is seen lying between the corpus callosum (*CC*) above and the optic thalamus below (*OT*). It consists of a heart-shaped median

part (*Fm*), with two lateral parts like wings (*Fl*), which are joined to the central part by a narrow isthmus which forms a sigmoid bend between them. The central part is made up of two halves, each of which contains in its upper part a small portion of grey matter, here stained yellow, which is in close contact with the under surface of the corpus callosum. This is evidently the remains of the septum lucidum, as has been already traced in fronto-oblique sections.

Situated just below the grey matter of the septum lucidum are some cut-across fibres, which are the median longitudinal fibres seen in horizontal sections (p 186). The lateral part of the fornix, or wing, has an irregular shape and is quite free in the lateral ventricle. The rest of the fibres in the central part of the fornix and also in the lateral part are arranged in such a confused manner that it is rather difficult to say what their course is, but for the most part they appear transversely cut at the inner part and obliquely cut at the outer part. The median part is gradually divided by a notch on its under surface into two halves.

This part of the fornix soon (fig 40) becomes flatter and more spread out along the under surface of the corpus callosum, and the notch which existed on the under surface between the two halves of the central median portion gradually disappears. The lateral parts (*Fl*) on either side, which are gradually extending, are now united to the central portion (*Fm*) by a still narrower isthmus, which makes here a more pronounced sigmoid bend. At the same time the shape of the lateral part alters, and it makes an angle where it rests on the optic thalamus.

The median part becomes thinner and more extended laterally, so that in fig. 40 it forms a narrow horizontal band (*Fm*) which is in contact with the under surface of the corpus callosum for its middle third (*C.C*), with which it becomes completely blended, and from which it can only be distinguished by the transversely cut appearance of its fibres, which are at right angles to those of the corpus callosum. The fibres of either side do not extend quite to the middle line. In the lateral part which extends to the outer limit of the lateral ventricle the direction of the fibres is obliquely downwards and outwards.

The next series of frontal sections extends from the anterior part of the pons to about its middle.

In these sections the corpus callosum has increased very much in thickness, and along the middle two-fourths of its under surface there is an exceedingly narrow band of transversely cut fibres. This arrangement, which is fairly well marked at the outer part of the middle third of the under surface of the corpus callosum, cannot be so definitely made out at the median line.

When traced outwards, this narrow band is seen to be connected with the two lateral parts or wings of the fornix by a faint sigmoid-shaped isthmus. This narrow band then, is evidently the continuation of the median portion of the fornix.

The lateral parts of the fornix are here very well developed. They lie in the lateral ventricle on each side, resting on the upper free surface of the optic thalamus and making an angle parallel to the upper surface of that body.

The direction of the fibres in the lateral part is oblique in the part nearest the middle line, and descending outwards and downwards at the external end. Above them a collection of vessels is seen in the lateral ventricle lying close to the nucleus caudatus, this is the choroid plexus on either side, whilst below the fornix and resting on the upper surface of the two optic thalami, is a membrane containing numerous blood vessels—the velum interpositum or the central part of the fold of pia mater entering the brain by the great transverse fissure between the fornix and the optic thalamus.

The lateral parts of the fornix are really what have been described as its essential parts, and it is the union of these two, at the middle line, which is considered to form what is known as the body, whilst the prolongations of these lateral portions, forwards and backwards, are known as the anterior and posterior crura respectively, and the latter crus subsequently becomes the *tænia hippocampi* or *fimbria*.

As we proceed further backwards in these sections, the sigmoid isthmus becomes straight. At the same time, the median fibres of the fornix, in contact with the corpus callosum, begin to interpose themselves between its lowest layer and a fresh set of fibres which have a transverse direction. The median tract cannot be traced completely across, but on the other hand a distinct septum, here stained yellow, is seen following the same course as the tract, but it is quite impossible to demonstrate the transverse commissural fibres of the fornix.

This layer of fibres, which is inferior to the median fornix and the septum, is the commencement of the splenium of the corpus callosum. If this be so, these transversely cut median fibres correspond to those fibres of the fornix which, in sagittal sections (p 182), pass between the main part of the corpus callosum and its splenium. After the median fibres of the fornix have been traced into the septum between the corpus callosum and its splenium, they gradually diminish until they disappear and the lateral fibres are alone left.

At the vertical level which we have now reached, the caudate nucleus is turning downwards to form the part known as its tail or surcingle, and, consequently, we can trace its grey matter from the part in the lateral ventricle above, to the tail in the descending cornu of that ventricle below. At the same time, the optic thalamus is almost detached from the cortical mantle, and the *tænia hippocampi* can be traced for a considerable distance downwards and outwards as it lies free in the lateral ventricle, between the optic thalamus and the caudate nucleus.

In the next series of sections, the optic thalamus and the pons are completely separated from the rest of the brain.

In the middle line, the corpus callosum is separated into two parts by a horizontal septum, viz., into the posterior part of the body and the splenium. Connected with this septum are the fibres of the fornix (which immediately becomes very much enlarged), passing outwards and downwards, in a thick bundle, to the cornu Ammonis.



The fornix, at its commencement here, lies to the outside of the splenium of the corpus callosum, whose fibres end abruptly at their outer part, and are stained a much deeper colour than the fibres of the fornix, and no communication can be traced between them.

We have reached here the vertical level where the main portion of the lateral ventricle is in direct communication with its inferior cornu, and it is along this communication that the fornix or *tænia hippocampi* can now be traced. Its fibres have a distinctly downward course, and on reaching the cornu Ammonis some of them enter the cell-layer of the cortex, while some of its outer fibres are prolonged along the outer surface of the cornu Ammonis, *i.e.*, that turned towards the lateral ventricle.

These last-named fibres form the alveus, and prolongations are sent from them into the cell-layer of the cornu Ammonis. The direction of these fibres at the upper part of the alveus, is *from* the cortex outwards and downwards, at the middle part they are transversely cut across, and at the lowest part, they assume a direction downwards and inwards from the cortex. They end in the bulbous-shaped fibres of the subiculum cornu Ammonis or, in other words, the central white matter of the temporo-sphenoidal lobe. In a more anterior section (fig. 40) these fibres (*Alv.*) turn downwards through the cingulum (*Cing. p.*) into the cortex of the temporo-sphenoidal lobe.

In another fronto-oblique section (fig. 41, right half) the corpus callosum (*C.C.*) is seen as a very wide mass of fibres. Here the posterior pillar of the fornix (fig. 41, right, *Fp.*) is seen as a thick band springing from the middle of the corpus callosum, *i.e.*, between its main part and the splenium, and coursing downwards along the lateral ventricle and on the outer surface of the optic thalamus to the cornu Ammonis where it is known as the fimbria (*Fimb.*), whilst on the other half of the section (fig. 41, left) which is the more posterior, the forceps major springs direct from the splenium.

The direction of the fibres of the fornix is a downward one corresponding to the long axis of its descending part.

Here again attention must be called to the difference in the depth of staining between the fornix and the callosal fibres, the light tint of the former being in marked contrast to the dark staining of the latter.

In fronto-oblique sections (figs. 42, 43, 44, right) through the posterior part of the corpora quadrigemina the descending pillar of the fornix and the forceps major of the corpus callosum (*Fp.*, *Spl.*) are in close apposition along the inner wall of the lateral ventricle. The fornix can be distinguished from the latter by its faint staining and by its apparent origin from the middle of the corpus callosum, whilst the forceps major is the direct continuation downwards and outwards of the splenium, and is stained as deeply as the rest of the corpus callosum. Therefore, as in sagittal sections, the descending pillar of the fornix lies just in front of the splenium and its



forceps major, so that in making a series of fronto-oblique sections from before back we at first cut through the fornix and behind that the splenium with its forceps major. It must be remembered that the descending pillar of the fornix is prolonged like a sheet along the whole length of the cornu Ammonis in the descending cornu of the lateral ventricle

We thus see in fronto-oblique sections, that the fornix is gradually encroached upon by the splenium and forceps major as we pass backwards, until at the level where the gyrus fornicatus has joined the gyrus hippocampi, the fornix has almost quite disappeared (fig 45, right)

In the next level (fig 41, left) the fornix has entirely disappeared, and in its place is the forceps major (*F M*)

*Summary* —As has been already mentioned, the part of the fornix here described includes the body, forming the highest part of the arch and the posterior crura. As the anterior crura will not be described, the account here given refers to the fornix after it has emerged from the septum lucidum to pass backwards as well as its arrangement in this part of the grey matter just before leaving it

While in the septum lucidum the fornix appears as a single tract of fibres (fronto-oblique sections), but just before leaving this structure it can be seen to separate into two sets of fibres, viz —(1) a median, (2) a lateral part.

The median part of one side is (frontal sections) joined to the corresponding part of the other side, being separated by a septum or raphe. The median fibres of opposite sides, together with the remains of the posterior part of the septum lucidum, form a structure which is as thick in a vertical direction as the corpus callosum. On either side the lateral part of the fornix is almost separated off from the median part, being merely attached by a narrow sigmoid band. Traced backwards the median fibres of either side, which throughout have a horizontal antero-posterior direction, are flattened horizontally along the under surface of the corpus callosum, and whereas the fibres of opposite sides were in contact with each other in front of the splenium, they gradually separate and pass into the septum between the corpus callosum and its splenium, and they can be traced into the substance of the corpus callosum (sagittal sections) in the septum as far as its upper and posterior surface, but how they leave this structure it is not possible to say. In the sagittal sections of a brain of the Monkey already referred to (p 161), fibres can be discerned passing through the corpus callosum almost like septa between the cut-across callosal fibres, and they are very similar to the course of the median fibres of the fornix in the corpus callosum of the Marmoset. But when these fibres are traced in the Monkey to the posterior and upper border of the corpus callosum, they appear to pass out of this body, and also at first to turn backwards and join the fibres of the cingulum, but on examination with higher powers of the microscope (*C, ZEISS*), it is not possible to make out a true connection between the two sets of fibres, the relations between them being more of the nature of a decussation. This appearance is only seen in the

sagittal section, where only a small piece of the cingulum remains in front of the posterior end of the corpus callosum

It is probable that these are the fibres referred to by MEYNERT and by HUGUENIN (see p. 181), as coming from the cingulum and passing through the corpus callosum to join the body of the fornix and so proceeding forwards. Whether they do come from the cingulum is, I think, not to be demonstrated. I am unable to find that either MEYNERT or HUGUENIN describe these fibres, which pass through the corpus callosum as a separate median bundle, remaining distinct as far forward as the septum lucidum from the lateral fibres coming up from the posterior crura

The lateral fibres of the fornix form that part which is usually described as the body its shape is at first rounded, it then becomes flattened in a horizontal direction, and diverges from the middle line, lying on the optic thalamus and between this and the caudate nucleus. And whereas the median part of the fornix is attached to the under surface of the main part of the corpus callosum, the lateral part is free in the lateral ventricle (frontal sections)

On reaching the splenium the lateral part of the fornix descends in front of this structure, lying between it and the optic thalamus

It is here rather difficult to separate the fornix from the splenium and its forceps major, which lie directly behind it, but the difference in staining by WEIGERT's method between the two is so marked that it gives considerable assistance. Moreover (fronto-oblique sections) the fornix appears to arise from the septum between the two parts of the corpus callosum, whereas the splenium is continued directly into its forceps major.

The descending part of the fornix, known as its posterior or descending pillar or crus, can be traced forwards along the descending cornu of the lateral ventricle to the anterior part of the hippocampus major or cornu Ammonis. In this course it is known as the *tænia hippocampi* or *fimbria*. It will thus be seen that the lateral part of the fornix forms a sheet of fibres extending the whole width of the lateral ventricle of each side, and this sheet becomes narrowed as it descends this cavity, being collected into the cord-like *fimbria*, from which again a very thin sheet, the *alveus*, is spread over all the cornu Ammonis.

Having now described the general arrangement of this part of the fornix it will be advisable to give a more minute account of the direction of its fibres, and their relation to the cortex of the cornu Ammonis.

In the body of the fornix the fibres of the median part are very irregular in direction, but for the most part they have an antero-posterior course. In the lateral part the fibres in sagittal sections appear in short lengths which have a direction downwards, outwards, and backwards, while forming the body they have no connection with surrounding grey matter, except the septum lucidum in front.

The posterior crus forms a roundish tract (knob-shaped on cross section) which takes

the course of the descending cornu, its fibres having at first a direction downwards and backwards, and then downwards and forwards

When the fornix reaches the antero-superior surface of the cornu Ammonis, it forms the fimbria and sends fibres into the cortex, and also a leash of fibres round the ventricular surface of the cornu Ammonis to the subiculum, this forms the alveus. We thus see that the cornu Ammonis is surrounded on three of its sides, viz, the supero-anterior, external, and infero-posterior, as well as on its anterior limit, by the different parts of the fornix, *i.e.*, the fimbria and alveus, which thus form a continuous sheet of white matter over those surfaces of the cornu Ammonis.

It is therefore not difficult, by examining frontal and horizontal sections, to explain how in sagittal sections made through the outer part of the cornu Ammonis, we see this structure to be oblong in shape, to diminish as we proceed outwards, and to be surrounded by a layer of fibres, the alveus. In sagittal sections the cornu lessens in extent from above downwards, from the fact that, as we descend in horizontal sections, it projects more into the lateral ventricle, and this lower part would therefore be the last to disappear in sagittal sections made successively from within outwards.

The direction of the fibres of the fimbria and the alveus is important, and it can only be made out by careful examination in all the three planes. To begin posteriorly, the fibres of the fimbria in sagittal and fronto-oblique sections (figs 11, 43) run in the plane of the latter section, *i.e.*, downwards and backwards, they are continued into the alveus in the same plane as far as the inferior surface of the cornu Ammonis, where the direction becomes more obliquely antero-posterior. It was found so very difficult to combine the appearances of the fimbria and the alveus into one mental picture, that it was necessary to make a model of the cornu Ammonis, and arrange the fibres according to their appearances already seen in the various planes. On doing this it appears that the fimbria forms a tract of fibres along the antero-superior aspect of the cornu Ammonis, having a direction parallel to its cortex, into which offsets are sent downwards and forwards as far as the horizontal level through the inferior surface of the occipital lobe, here (as seen in horizontal sections) the direction of the fibres changes, and they then course from the cortex of the cornu Ammonis forwards and then downwards round the anterior extremity of this structure, to end in the cortex on the inferior surface of the temporo-sphenoidal lobe, these fibres, in front of the cornu Ammonis, are really part of the alveus, which has the following arrangement.—At the posterior end of the cornu Ammonis, as stated above, some of the fibres from the fimbria pass into the alveus, and wind round the outer surface of this cortex to its under surface, where they are directed forwards and downwards, in front of this part the alveus receives fibres from the cortex of the cornu Ammonis, around which it winds till the under surface is reached, when the fibres turn downwards towards the cortex of the under surface of the temporo-sphenoidal lobe.

It would thus appear that, whereas the direction of the fibres of the fimbria is from behind forwards into the cell-layer of the cornu Ammonis, the direction of the alveus is from this cortex downwards to end in the medullary centre of the inferior surface of the temporo-sphenoidal lobe

A few words must now be said with regard to the transverse fibres of the fornix, which have been described by authors as forming a commissure between the cornu Ammonis of opposite sides. It was remarked, in describing the fornix in the three different planes, how difficult it was to separate the splenium from the fornix, which lay beneath and in front of it. This was particularly the case with the horizontal and fronto-oblique planes (*cf* figs 30, and 44 right), where it was only possible to arrive at some separation between the two sets of fibres by the difference in the amount of staining by WEIGERT'S method. On looking at sagittal sections near the middle line (figs 1 to 4), it will be found that no transverse fibres exist in the neighbourhood of the posterior part of the body of the fornix except those of the splenium. I can only suggest that the transverse fibres seen in the horizontal sections may pass across to the opposite side with the splenium proper, and these may form the anterior and inferior part of the triangular bundle of the splenium (fig. 4) which is stained a much paler tint than the rest of the fibres, and be commissural between the cornua Ammonis of opposite sides, for no fibres can be traced into them from the forceps major. It must be stated that no transverse fibres of the fornix could be traced across the middle line in frontal sections.

I would again call attention to the manner in which the fornix is stained by WEIGERT'S hæmatoxylin method. In all the sections made in different planes, and of course from different brains, the fornix is always stained of a much lighter tint than that of the internal capsule and the corpus callosum. Whether this is due to a less development of the myeline sheath—the structure stained by the hæmatoxylin—I am not prepared to say, but it does not seem to be caused by a looser aggregation of the fibres, as individual fibres of the internal capsule are as deeply stained as when they are in compact bundles. In connection with this subject it is interesting to note the structure known as the tænia semicircularis, which lies in the floor of the lateral ventricle between the caudate nucleus and the optic thalamus, just outside the body of the fornix. It is seen as a round bundle of fibres in sagittal and frontal sections (figs. 5–10, 40, *TS*) and as a narrow band in horizontal sections (fig 23, *TS*) which is exceedingly faintly stained, just in front of the fornix and between this and the tail of the caudate nucleus, and it seems to consist of little more than fibrous tissue. It is suggested that it is the degenerated remains of a structure once more highly developed. We therefore appear to have three sets of fibres differing in their powers of being stained by this method, viz, those which are strongly coloured, as the corpus callosum; those which are less well stained, the fornix and also the cingulum, and those which are hardly stained at all, the tænia semicircularis.

## EXPLANATION OF PLATES 20-24

(The same letters apply to all the figures )

*Alv* Alveus of Cornu Ammonis

<i>Cing</i> {	<i>a</i>	}	Cingulum	{ anterior part
	<i>h</i>			{ horizontal part
	<i>p</i>			{ posterior part

*CA* Cornu Ammonis or Hippocampus Major.*CC* Body of Corpus Callosum*FM* Forceps major posterior of Corpus Callosum*Spl* Splenium of Corpus Callosum.*Spl'* The part intermediate between the Body and the Splenium*Tap* Tapetum of Corpus Callosum*C.E* Capsula Externa*Cf* Calcarine fibres*Cge* Corpus geniculatum externum*CI* Capsula Interna*CN* Caudate Nucleus*cn* Tail of Caudate Nucleus or Surcingle*Cq.* Corpora quadrigemina*CR.* Corona Radiata.*Cer* Cerebellum*Cr* Crus Cerebri*F* Fornix*F<sub>i</sub>* Fibres of Fornix internal to Optic Thalamus*F<sub>l</sub>* Lateral fibres of Fornix*F<sub>m</sub>* Median fibres of Fornix*F<sub>p</sub>* Posterior descending pillar or crus of Fornix*Fimb* Fimbria or Tænia Hippocampi of Cornu Ammonis*FC.* Fissura Calcarina*For M* Foramen Monroi.*GF* Gyrus Fornicatus*H.L* Hippocampal Lobule containing the Nucleus Amygdalæ.*H.S* Hippocampal or Dentate Sulcus.*LN* Lenticular Nucleus*LV.* Lateral Ventricle*L.V.d.* Descending Cornu of Lateral Ventricle.*L V<sub>p</sub>* Posterior Cornu of Lateral Ventricle.

*O Ch* Optic Chiasma

*O T* Optic Thalamus

*O t* Optic tract.

*S F* Fissure of SYLVIVS.

*S f* Superficial fibres of Gyrus Fornicatus and Gyrus Hippocampi, or superficial medullary lamina.

*S L* Septum Lucidum

*T S* Tænia Semicircularis.

### DESCRIPTION OF THE FIGURES

#### PLATE 20

Figs 1-4.—Photographs of microscopic sections of the brain of the Marmoset (*Hapale penicillata*) cut in the sagittal direction and stained by PAL's hæmatoxylin method. The medullated fibres are stained black, and the grey matter is of a grey colour. Fig. 1 is made a short distance from the middle line, and the other sections are external to it. Magnified three diameters.

#### PLATE 21

Figs 5-10.—Photographs of similar sections of *Hapale penicillata*. Sagittal direction. Stained by WEIGERT's method. Magnified three diameters.

#### PLATE 22.

Figs 11 and 12.—Photographs of sections of *Hapale penicillata*, sagittal direction. Stained by PAL's method. Magnified two diameters.

Figs. 5-12 represent levels progressing gradually outwards.

#### PLATE 22.

Figs 13-15.—Photographs of sections of the right hemisphere of *Hapale jactans*. Horizontal direction. Stained by WEIGERT's method. Magnified two diameters.

Fig 13 is the most superior, and is taken a short distance below the highest point of the centrum ovale.

## PLATES 22, 23

Figs 16-34 —Photographs of sections of the right hemisphere of *Hapale jactans*  
Horizontal direction Stained by WEIGERT's method Magnified two  
diameters

A greater interval exists between figs 22 and 24 than in the other  
figures

## PLATE 23

Figs 35-38 —Photographs of sections of the right hemisphere of *Hapale penicillata*  
Horizontal direction. Stained by PAL's method. Magnified two diameters

## PLATE 24

Figs. 39 and 40 —Photographs of sections of the brain of *Hapale jactans* Frontal  
direction. Stained by WEIGERT's method *in toto*

Fig. 39 is taken through the optic chiasma, fig 40 is immediately  
anterior to the pons Varolii. Magnified two diameters

## PLATE 24

Figs 41-45 —Photographs of sections through the corpora quadrigemina of the brain  
of *Hapale penicillata* Fronto-oblique direction Stained by WEIGERT's  
method Magnified two diameters

The two hemispheres are not cut at quite the same level, the right being  
more anterior than the left, so that the right half of fig 45 is anterior to the  
left half of fig 41, thus giving the appearance of ten levels from before  
backwards

N B.—In fig 29 the line from *F.M* should be continued to the white dot behind  
the cornu Ammonis

In fig 34 the line from *F.M.* is carried too far beyond the forceps major to the  
cingulum, which the line from *Cing. p.* should reach

In fig 39 the line from *Fm* should be continued to the white dot in the fornix  
beneath the corpus callosum to which it points, while the line from *CC* should be  
continued on to the corpus callosum, the line from *Fl.* ends at the eighth white dot,  
and external to it is a black dot, where the line from *LV* should end

In fig 40 the line from *LV.* should be continued to the dot internal to the line  
from *cn*

In fig 41 the line from *Spl* should be continued to the white dot on the inferior  
part of the corpus callosum. the line from *FD* ends in the eighth and not the sixth  
white dot, the line from *FC* ends in the black dot on the grey background, the  
line from *H.S.* ends in the sixth white dot





IV *On the Changes produced in the Circulation and Respiration by Increase of the Intra-cranial Pressure or Tension \**

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*Introduction*

FOR some time we have made intra-cranial pressure the subject of an enquiry. The present paper deals with the effect upon the circulation and respiration of an increase of such intra-cranial pressure. Our object is to indicate how the degree of the intra-cranial tension may be estimated by changes in the pulse and breathing, whether a prognosis may be formed as to the termination of the condition, and whether the effect is due to gradual loss of function of the lower part of the medulla.

Until lately, the pulse and breathing have yielded signs, the meaning of which was uncertain, thus the pulse, it is said, may be slow and of low tension, or again, in severe cases, quicker than normal and of high tension. The respiration also, is sometimes noted as being stertorous, or of the “Cheyne-Stokes” rhythm. But although death frequently comes by arrest of respiration in tumours of the brain, whilst the heart may continue to beat for five, ten, or even thirty minutes after, little has been recorded concerning the abnormal rhythm of respiration preceding its arrest; we

\* The expenses of this investigation were defrayed by a part of a grant of money made by the Royal Society

† I wish to take this opportunity of saying that the bulk of the labour of making and collating the records in this research has been performed by Mr SPENCER—V H

therefore arranged our experimental method so as to investigate these phenomena in their entirety. It is impossible to give a full explanation of all the results we have obtained, because the functions of the medulla are not yet fully understood, and therefore, whatever hypotheses we have advanced on these points in this paper, have been inserted merely for the sake of clearness, and are fully open, of course, to future revision. However, the recorded tracings of all the experiments show so clearly that a diminished activity of the medulla occurs as a definite sequence of events contemporaneously with increase in the intra-cranial pressure, that we regard this fundamental fact to be established, therefore the value of the results, as regards the estimation of the effect of increased pressure, is independent of exact knowledge of the mode of their production. Further, we believe that our experiments have an important general bearing, in that they show how the three "centres" regulating the heart rate, the blood pressure, and the respiration, can be impeded or arrested, either together, or almost separately, and consequently the varying influences they have the one on the other can be estimated with an approximation to accuracy.

## 2 *Historical Retrospect.*

Of course an immense number of researches have been made in investigation of the general subject of intra-cranial pressure and compression of the brain, but for the present purpose, with the view of avoiding confusion, we have selected only those observations which directly bear on the object of the present communication.

LORRY, in a research,\* compressed the skulls of young animals and produced unconsciousness. Also, he inserted a curved instrument through the membrana obturatoria. When he pressed the cerebellum down on the medulla the animal fell into a deep sleep, when he turned the instrument round and touched the upper end of the spinal cord, the animal awoke and became convulsed.

ASTLEY COOPER† made a very suggestive experiment bearing on this point, he trephined a Dog and pressed with his finger upon the dura mater, the Dog became insensible, then comatose, and the pulse slow. When the pressure was relaxed the animal recovered consciousness completely.

LEYDEN‡ was the first to record the changes in blood pressure by a series of experiments, in which he raised the intra-cranial pressure with a piston fitting into a collar which had been screwed into the skull, the pressure on the piston being measured by a column of mercury. He noted the slowing of the pulse and, later on, its great rapidity, also the deep stertorous respiration, its final arrest, and the effects of division of the vagi on the pulse rate.

\* "Sur les Mouvements du Cerveau et de la Dure-mère, 2<sup>me</sup> Mémoire" 'Mémoires de l'Académie des Sciences — Sav. Étrang,' vol. 3, 1760, p. 344

† 'Lectures on Surgery,' 1824, vol. 1, p. 300.

‡ VIRCHOW'S 'Archiv,' 1866, vol. 37

DURET\* injected wax in order to increase the intra-cranial pressure. In one experiment, when he injected a large quantity of wax into the cranial cavity of a Dog, respiration ceased, but as soon as the occipito-atlantal ligament (*membrana obturatoria*) was incised, the subarachnoid fluid spurted out in a stream, 50 to 60 mm high, and the Dog began to breathe again. DURET also found that when the pressure of the injected fluid was increased from 18 to 27 mm Hg, the pulse frequently sank from 83 to 13, and the blood pressure increased to 160–220 mm Hg, or even higher, and further, that when the pressure of the injection was 27 to 33 mm. Hg, the pulse increased in frequency. Diminution of the intra-cranial space amounting to 5 per cent of its content, when the injection was subdural, produced somnolence and coma, and 8 per cent decrease of the space produced death in a few hours.

PAGENSTECHE† found that the cranial cavity could be reduced by wax measuring 2.9 per cent. of its content, or even in some cases 6.5 per cent, without any symptoms being caused.

FRANÇOIS FRANCK‡ made a series of experiments which showed that (1) a sudden increase of pressure in the intra-cranial arterioles produced slowing of the heart beats, (2) the increase of intra-cardiac pressure had the same result.

For this experiment he isolated the cerebral circulation in the Dog by ligature of the four arteries in the neck and kept up an artificial circulation of defibrinated blood through the brain. When a regular rhythm of the heart appeared he raised the pressure of the circulation through the distal end of the carotid by 4 cm Hg. The result was an arrest of the heart with a great fall of blood pressure. The arrest of the heart lasted three seconds and then the beats regained their former frequency. He further found that, even when the cerebral circulation was not cut off, if defibrinated blood were sharply injected into the peripheral end of the carotid in a Dog an arrest of the heart could be produced, and that when the artificial circulation was in action the result of obstruction to the outflow through the jugular veins was the same as when the pressure of the inflowing fluid was raised.

He also raised the intra-cranial pressure in another way.

He screwed into a trephine hole a collar which was closed below by a membrane of caoutchouc and which was connected at the external end to a pressure bottle and manometer. He employed air as the agent of compression, the membrane preventing the air from reaching the veins, and at the same time, by distending, providing for the required diminution of the intra-cranial space. He found that gradual compression of the surface of the brain produced slowing of the heart and of the respiratory movements. These effects were produced before the height of the compression reached that of the blood pressure.

\* 'Traumatismes Cérébraux,' Paris, 1878.

† 'Experimente und Studien über Gehirndruck,' Heidelberg, 1871.

‡ 'Travaux du Laboratoire MAREY.'

BERGMANN\* injected wax and found the pulse became slower as 3 is to 1 2, or as 3 is to 1, and that the blood pressure was slightly raised above the normal as 1 is to 1.1, or as 1 to 1 2. The ascent and descent of the blood pressure with each heart beat was greater than normal, and the apex of each curve more rounded, owing to the prolongation of the systole. After division of the vagi the injection of wax produced still greater rise of the general blood pressure. BERGMANN also observed the result of compressing a sacral meningocele in a Child. The Child, at first restless, passed into a deep sleep, while with further compression the slow respiration became irregular. Finally the respiration was arrested for ten to twelve seconds, and then began as in "Cheyne-Stokes" respiration, to end in another pause. Meanwhile the pulse sank from 120 or 100 to 50 or 40.

NAUNYN and SCHREIBER.†—These authors produced general increase of subdural and subarachnoid tension by injecting fluid under known pressure as measured by a mercury column. If they applied rapidly a severe pressure the pulse rate notably slowed and the respiration gradually disappeared, the respiration usually slowing before the heart. If the pressure were slight and applied slowly the respiration became slowed but did not cease, and the blood pressure was raised. If the pressure were continued and increased the respiration gradually stopped as before, and it was occasionally necessary to employ artificial respiration to prevent a fatal termination. They noticed vasomotor curves of various kinds, the chief of which were (1) rhythmical variations in the mean pressure, and (2) curves commencing while the heart was slowed and disappearing as soon as the pressure was taken off. They never seem to have got the true acceleration of the heart after long continued and severe pressure. With the slowing of the heart they do not appear to have caused much fall of blood pressure nor arrest of the heart, apparently the rise of blood pressure generally obtained was aided by the large amount of fluid which was perfused into the animal. Thus as much as 400 c.c. passed into a Dog of  $9\frac{1}{2}$  kilos in  $1\frac{1}{2}$  hour.

SCHULTEN‡ found in a Rabbit that when the intra-cranial pressure was raised to 140 mm. Hg, by injection of salt solution, arrest of respiration took place. When the pressure was below that of the blood all that was obtained was a small rise of the blood pressure. When this was continued, exaggerated and slowed vagal heart beats were produced. This slowing of the heart beat was converted into acceleration when the blood pressure fell and a fatal termination appeared imminent. He ascribed this to simultaneous paralysis of the vagal and vasomotor centres.

He like PAGENSTECHER and DURET, further found that the symptoms of intra-cranial pressure were produced when the cranial content was diminished by more than six to seven per cent.

\* "Kopfverletzungen," 'Deutsche Chirurgie,' Stuttgart, vol. 30, 1886.

† 'Archiv für Experimentelle Pathologie und Pharmakologie,' 1881, vol. 14, p. 1.

‡ 'Archiv für Klinische Chirurgie,' 1886, vol. 32, p. 455.

SCHWARTZE\* compressed the skull in young animals (Rabbits) and observed the heart directly through an opening in the thorax, artificial respiration being maintained. He found that increase of intra-cranial pressure produced, without damage to meninges or cerebrum, immediate and marked slowing of the heart.

### 3 *Anatomical and Physiological Considerations*

Before commencing a description of the methods we employed and the results obtained, it is absolutely necessary to discuss certain considerations respecting the various anatomical alterations produced by the increase of pressure, as well as the probable manner in which such pressure acted, both directly upon the surface of the brain, and indirectly upon deeper parts at a distance, *e g*, the bulb, &c, reflex effects being excluded by the anæsthesia.

The skull and spinal column enclose the brain and cord in a rigid cavity perforated by numerous holes. During life blood enters by the arteries and escapes by the veins, the cerebro-spinal fluid being drained off by the numerous lymphatics (*vide* AXEL-KEY and RETZIUS†) which pass out through the foramina along with the nerves and other structures. Between the arterial circulation and that in the veins, and the lymph of the lymphatics, is placed the subarachnoid fluid.

The subarachnoid space is continuous throughout the cranium and freely communicates through the foramen magnum with the space in the spinal cord. An increase of the subarachnoid fluid pressure is well known to render its absorption more rapid, at the same time that the transudation of fluid from the capillaries is diminished. Hence, when the pressure of the subarachnoid fluid is raised there will be a tendency to return to the normal tension. If the increased pressure be due to part of the subarachnoid space being occupied by a foreign body, then the return to the normal tension will be reached as soon as an amount of subarachnoid fluid, corresponding to the volume of the subarachnoid space occupied by the foreign body, has been removed by absorption. If the subarachnoid fluid pressure be raised it may reach the height of the blood pressure in the capillaries supplying the cells of the cortex of the brain. If the pressure in the subarachnoid space pass beyond this point it will diminish the blood supply to the cortical cells, and if increased further, the capillaries will become obliterated, and so the circulation in the cortex be cut off altogether.

Here then we have at once a mode in which by general increase of the intra-cranial pressure, *i e*, of the cerebro-spinal fluid, failure of the function of the nerve cells in the cortex is produced. This also applies, no doubt, to the grey matter of the central ventricular axis, and we believe this to occur, the more especially since the valuable

\* 'Archiv für Gynakologie,' 1870, vol 1, p 36

† 'Studien in der Anatomie des Nervensystems,' 1st part, Stockholm, 1875

results obtained by DURET\* (and from which he derived his principle of "choc céphalo-rachidien") give evidence of the communication by the cerebro-spinal fluid filling the central canal, translating the pressure applied on the outside to the centres in the grey matter lining the ventricles

Bearing closely on this point, but also far more on the next to be discussed, are the researches made by GRASHEY† into the compressibility of the brain substance. These show at once that the effect of general increase in the intra-cranial pressure must be the speedy communication of the same to the centres in the floor of the fourth ventricle

But it also occurred to us that another and totally different *modus operandi* of pressure, producing changes in the circulation and respiration, might be found in the direct pressure of the brain substance transmitted, like all pressure in solid bodies, in a straight line to the bulb, *i.e.*, to the nerve corpuscles constituting the vagal and other nuclei‡

If such direct pressure be produced either by a foreign body, by depression of the skull, or by hæmorrhage, the circulation in the part of the brain compressed is impaired. If the force of compression be less than the blood pressure in the capillaries, the circulation will be only impeded, if greater than that in the capillaries, the circulation will of course be cut off

Bearing upon this point, we may now mention that in a series of experiments not yet published, in which varying pressures were made on a circumscribed portion of the cerebral cortex by discs of glass inserted under antiseptic precautions, we observed that apparently in some instances compensation on the part of the cerebro-spinal fluid enabled the capillary circulation to be completely restored. This introduces at once a new factor for consideration under the present heading, *viz.*, the question of the time interval required for the fulfilment of such compensation. In the researches which are the subject of the present paper, we have not regarded this important point with so much consideration as the more important one of determining what are the gravest, *i.e.*, the severest alterations in the circulation and respiration produced by rapid increase of the intra-cranial pressure

These points being clear, there remains yet another possible way in which the blood supply to a compressed part may be provided for, besides that by compensation for the subarachnoid fluid. Thus we have reason to believe that we have seen circulatory compensation brought about by a rise in the general blood pressure, and

\* *Loco citato*

† "Ueber Hirndruck und Hirn-Compressibilität" 'Sitzungsberichte der Physico-medizinischen Gesellschaft zu Würzburg,' 1885, p. 139, and 'Allgemeine Zeitschrift für Psychiatrie' Berlin, 1886, vol. 43, p. 276

‡ FRANÇOIS FRANCK (*v.* "History") suggested in 1877 that the effects observed were probably due to "l'action mécanique de la compression sur les éléments nerveux et à un degré plus avancé l'anémie encéphalique unie à la première influence qui l'a déterminée et qui continue à s'exercer."



consequently a restoration of function effected in spite of the persistence of the compression.

We have alluded above to the direct communication through the brain substance in accordance with the laws of the transmission of pressure through solid bodies. It will have occurred to some who have studied this question that notice should be taken of the possibility of the cerebral hemisphere, if not the whole brain, moving *en masse* when pressure is applied in the cranial cavity at any particular point. This implies the possibility, for example, of pressure on the fore part of the brain, driving the fore part of the brain back on the occipital part, and this latter on the tentorium. This leads necessarily to the possibility of the tentorium interfering notably to the protection of the subtentorial part from pressure in the region of the cortex.

All these considerations will receive in the description of our results a detailed analysis.

#### 4 *Modes of Investigation.*

*Animals*—We have used Dogs mainly, but we have also used a few Monkeys (almost invariably *Macacus rhesus*, more rarely *Macacus sinicus*), and we hope to extend our researches on Monkeys in order to make them more closely analogous to diseased conditions in Man.

*Anæsthetic*—We have employed in all cases complete anæsthesia. There is, therefore, an absence of all changes due to consciousness, reflex effects, or convulsions. Ether has been the anæsthetic used, the circulation and respiration having been steadily maintained along with complete anæsthesia. The Dog was first rendered unconscious by a mixture of equal parts of ether and chloroform. Then a tube was placed in the trachea, to which a rubber tube was attached, and at the other end of the rubber tube a funnel. An ordinary sponge-bag, half full of cotton wool, received the ether, and the funnel was inserted into the sponge-bag. By drawing the neck of the bag around the funnel to varying degrees of tightness, we found that we could regulate the proportion of air to ether. In this way the narcosis can be regularly maintained in the Dog with a moderate amount of ether. Furthermore, artificial respiration was supplied through the trachea tube when required.

*Mode of Recording the Respiratory Movements.*—We recorded the movements of the lower part of the thorax by means of a PAUL BERT's respiratory drum and tambour. This gives, of course, correctly the expansion, &c., of the chest, but does not differentiate between the action of the diaphragm and of the other respiratory muscles. In all our tracings, the up stroke of the lever takes place in inspiration, and the down stroke in expiration.

*Mode of Recording the Circulation.*—A recording mercury manometer was used for this purpose, connected with a cannula in the carotid. We also, occasionally, used a FICK's spring kymograph, but since every forcible heart-beat produced a violent

excursion of the lever, an accurate tracing was scarcely possible when the blood pressure rose very high. We consequently confined ourselves to the use of the mercurial manometer. Since we found that clotting frequently took place in the femoral, especially when the venosity of the blood was increased, or when there were great changes in blood pressure, we put the cannula in the carotid on the cardiac side. The cutting-off of one carotid does not, we believe, materially diminish the circulation in the brain of the Dog. The writing point of the manometer was placed vertically above or below that of the respiratory lever when at rest.

The respiratory and manometer traces were simultaneously taken on a three-metre continuous travelling smoked surface, so that the whole course of the experiment, from the application of the compression to its removal and the recovery from its influence, could be included. The rate was about 14.5 cm. per minute, and each trace is to be read from left to right.

*Method of Raising the Intra-cranial Pressure* — After various attempts, we found the following the most satisfactory:—Thin-walled, easily-distensible india-rubber bags were obtained, both pear-shaped and globular. Each bag was continuous at its neck with a stiff steel thin-metal tube, about 12 cm. long and 3 mm. diameter. The other end of the metal tube was connected with the lower end of a burette by means of very thick-walled rubber tubing, which was not distensible with the pressure we employed. The burette was filled with mercury after all air had been exhausted from the rubber bag and tubing, so that when the bag was held at the level of the surface of the mercury in the burette, or rather above the level, the vacuum in the bag made it occupy the smallest possible space. When the burette containing the mercury was raised above the level of the bag, the bag immediately became distended by the mercury, and when the mercury was lowered, the bag of course immediately collapsed. If the distension of the bag were unimpeded, only a very small column of mercury was necessary to distend it, on account of the elasticity of the rubber. Therefore, when the bag was introduced into the closed skull, the amount of force required for the mere distension was neglected, as being so extremely small. Consequently, it follows that the degree to which the mercury sank in the burette, and the height of the level of the mercury above the surface of the brain, accurately represented respectively the volume of the distended bag and the degree of pressure employed. Thus the distension of the bag diminished the cranial content, and the amount of diminution was indicated in cubic centimetres by the amount of mercury which had escaped from the burette. In this way pressure on the brain could be applied slowly or rapidly, at will, to any desired amount as measured in millimetres of mercury; and by lowering the mercury column below the level of the bag, all compression of the brain could be instantly removed, and the bag reduced to occupy an unappreciable space on account of the vacuum thus produced in it.

The collapsed bag was inserted through a centimetre trephine hole, and was fixed in position by a plate of metal, perforated in the centre for the passage of the metal

tube attached to the bag. The plate closed the trephine hole, and prevented any bulging outwards of the bag or any protrusion of the brain

The bag was inserted at various points from the supra-orbital region in front to the cerebellar region behind, as will be described later. It was first placed between the skull and the dura mater, the latter remaining intact; later, between the dura mater and the brain; and, finally, in the substance of the brain, and where necessary in the cavity of the fourth ventricle.

In order to reclose a trephine hole, a steel plug of the same diameter as the trephine was screwed tightly into it.

Another method of raising the intra-cranial pressure was to compress the skull as a whole. This, naturally, was only possible in young animals. The intact skull in Puppies was compressed for this purpose in various directions, and the amount measured by the diminution in diameter of the skull between the points compressed. As a matter of fact the results thus obtained did not differ materially from those produced by the bag pressure, and consequently are not detailed further.

The effects of intra-cranial hæmorrhage were employed as a means of pressure when the compression by the bag had injured some vessel, which bled when the pressure was removed from the bag. Also, intra-cranial vessels were intentionally divided, and the trephine hole closed through which the division had been made.

## 5 RESULTS.

### *a General Observations*

In summarising the general results we have obtained, we may first advert to the method of experiment as we found it to work practically. In the first place, if the bag were inserted between the bone and the dura mater, it was obvious from the slow distension of the bag that the separation of the dura mater from the bone was being gradually accomplished. Moreover, of course the resistance of the uninjured dura mater is considerable, seeing that that membrane shrinks somewhat when separated from the bone, and does not hang loosely, except when extensively detached. We are thus brought to consider the results of our increase of intra-cranial pressure according to the two points of view, as to whether the pressure was effected slowly or quickly. In the following experiments it will be found that we have frequently varied the rate at which the additions to the intra-cranial pressure were made. On the whole the intra-cranial pressure was applied rapidly, a maximal amount having effect generally within five minutes, and frequently within a much shorter interval.

We have next to consider the modes by which the increase of pressure on the one hand and the removal of the pressure on the other showed themselves. Although the moments of commencing and relaxing the pressure respectively were recorded on each tracing, it was from the first evident that, whereas it was comparatively easy to detect

the effects produced by the incidence of the pressure, it was by no means so easy to determine the mode of recovery after the pressure had been completely relaxed. The reason of this last difficulty we must now discuss. To those who have made observations on compression of the brain it will be easy to understand that, if the pressure applied had been considerable, and if the blood pressure were low, the brain would not react immediately upon the withdrawal of the pressure. This non-reaction, characterised by the brain remaining excavated (through the pressure of the bag, &c), is that which we must now analyse. From other experiments, which we shall mention directly, it is clear that such excavation of the brain substance cannot of itself afford inhibitory or excitatory impulses passing down to the respiratory and circulatory centres in the medulla. This view of the facts points to the effect being due to the mechanical principles before alluded to (See p 205)

That this is true is shown also by another observation which we have made in a different manner, as follows. If pressure were applied very slowly it was easy to produce a considerable amount of such excavation as that referred to, without bringing about any effects, or only slight effects which were easily recovered from.

This introduces us to the consideration of the question of *compensation* in connexion with the origin of the effect. All the experiments show that a certain diminution in the cranial cavity has to be attained before the pressure effects begin to show themselves. This preliminary diminution, measured absolutely, has we find in most of our experiments been 5 c c. This is the average absolute diminution of the cranial capacity which must be brought about before pressure effects appear. This interesting point has been made the subject of observations, notably by PAGENSTECHER and DURET. These authors approached the subject from the point of view of relative diminution of the whole cavity. The chances of error in making observations of this kind are we think considerable, and demand very special attention. Although we have carefully preserved all our material, viz, brains, skulls, &c, for this object, we have nevertheless thought it best to leave the consideration of the relative values until we can devote special attention to the point: we desire, however, to consider the matter a little further on account of the remarkable constancy of the phenomenon. With our apparatus, the value obtained, *e.g.*, 5 c c., must obviously mean the overcoming of certain resistances. These resistances we believe to be —

1. Resistance to the outflow of cerebro-spinal fluid from the cranial cavity
2. The resistance (*i.e.*, of the blood pressure) to the emptying of the blood vessels of the part of the brain immediately pressed upon
3. The natural elastic resistance of the brain substance
4. The resistance to mass displacements.

Of the last two we unfortunately know nothing, although we have commenced a research into this little known subject. Of the remaining two the resistance more easily overcome is that of the blood pressure

In this connexion we have performed a distinct series of experiments to contribute to our present knowledge on the subject, in the following manner. Supposing the foregoing considerations to be true, it seemed clear that we could have with ease a control experiment if we first diminished the intra-cranial space by some constant amount, and then commenced the application of pressure. As might have been expected the effect was to render the bulbar centres extremely sensitive. To such a degree did this sensitiveness go, when preliminary diminution of the intra-cranial space had been carried out, that the additional diminution of 0.5 c.c. or 1 c.c. was sufficient to cause arrest of the heart.

On the other hand it became more difficult to affect the circulation and respiration, or a higher column of mercury was required to distend the bag, if more than one trephine hole were made. And this was especially the case if the dura mater were divided in addition, for then the brain bulged into the other trephine holes. Also if part of the occipital bone was removed, so that the cerebellum might bulge, or the occipito-atlantal ligament divided, and fluid could escape whenever the cerebrum was compressed, the functions of the medulla were able to recover.

*The mass displacements of the brain* referred to above we may now turn to. When pressure is applied to the cerebral hemisphere, especially above and in front, we have such displacement of the encephalon that in spite of the support given by the tentorium (which it is to be remembered is bony for the most part in the Carnivora) the cerebellum is driven through the foramen magnum. Consequently, the removal of the pressure effect is readily accomplished by trephining the occipital bone, and raising the vermiform process so as to lift off the compression which it is effecting upon the medulla.

### *Direct Mechanical Influence upon the Medulla*

We are now brought to the final consideration of a very interesting question we raised on p. 206, viz., the possibility of the pressure effect being in part due to excitation at the point of the brain chiefly pressed upon. From the facts which we have related on p. 209, there was no reason to believe that such an excitatory effect existed. But we now wish to mention a direct experiment which we made in connexion with this subject, and that of mass displacement. The experiment consisted of division of the mesencephalon, after which it was found that pressure was just as active as before in calling forth the changes in the circulation and respiration.

The effects observed are consequently not due to any local excitation at the point chiefly compressed.

### *b Details of Observations*

The extreme difficulty of collating such an enormous number of observations as those which we have at our disposal has led us to adopt the following method of classification and arrangement of our results.

One special feature of our experiments has been the application of pressure in different regions of the brain. This we have done for a special purpose which we do not allude to in the present paper, since we do not feel ourselves to be in possession of facts, even yet, whence to draw accurate inferences. However, by moving the point of pressure we have found that additional light has been thrown upon the subject of the present paper, for the effects obtained by the application of the pressure directly to the fourth ventricle have proved so clear, that we have separated them into a distinct class of observations, and used them to explain the results of the application applied to any part of the brain. Therefore, the first great division of our results is as follows.—

DIVISION A.—Effects of pressure applied to any part of the cerebral and cerebellar hemispheres

DIVISION B.—Effects of pressure applied directly in the fourth ventricle

It next became necessary to further subdivide these primary divisions. The way that seemed most feasible to us was to take some prominent phenomenon and hang, as it were, the observations upon it. The phenomenon in question which we selected was the classical one of slowing of the heart. In this way it was possible to subdivide DIVISION A, as follows.—

DIVISION A.—Pressure applied to any part of the surface of the cerebrum or cerebellum	(1) No marked slowing of heart. . .	{ H. Heart. V. Blood pressure. R. Respiration.
	(2) Slowing, arrest, and recovery of heart	{ H. Heart. V. Blood pressure. R. Respiration.
	(3) After division of the vagi. . .	{ H. Heart. V. Blood pressure. R. Respiration.

DIVISION B —Pressure applied in the fourth ventricle, with consequent differentiation of pressure effects.

The observations under each sub-division are grouped according as they relate to the heart, blood pressure, and respiration, respectively.

These we have designated by the initials H for heart, V for blood pressure, and R for respiration

We hope, therefore, in the account of our observations which we shall give immediately, that the headings of each sub-division will be comprehensible.

DIVISION A. *Pressure applied to any part of the brain.*

(1) Pressure insufficient to produce marked slowing of the heart.

H. *Rate of heart.*—We have observed the following changes in the rate of the



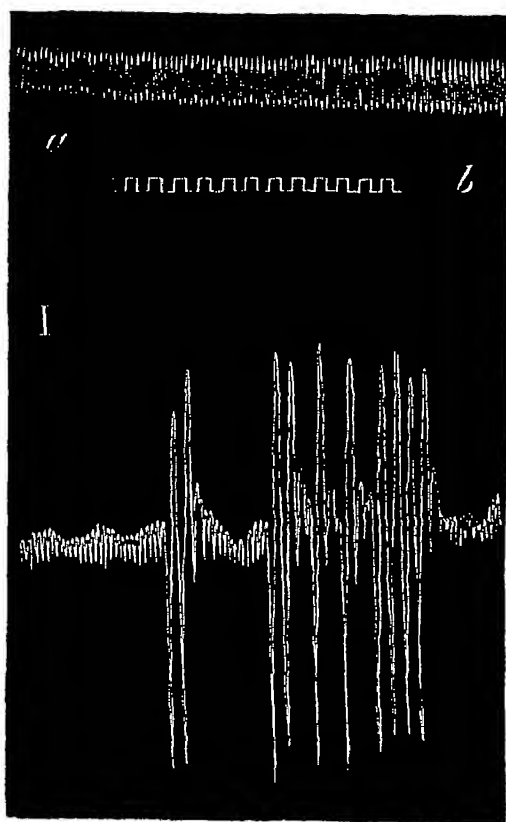
heart beat to occur under the above circumstances. A slight pressure may cause the same effect as that which results from putting the animal deeply under ether, *i e.*, the heart rate may be diminished from 180 or 190 per minute to 130 or 120 per minute.

Less pressure is required to slow the heart when there is deep etherisation, conversely, less ether is required to arrest the respirations and slow the heart when pressure has already been applied.

*Intermissions in the heart beat.*—Occasionally intermissions were observed immediately on the application of the pressure, which recurred some ten times soon after the commencement. In the same experiment there were also three instances of this during the recovery from the first application of pressure.

The following experiment exhibits these phenomena (see Tracing I.) :—

Tracing I



The upper line is the Respiratory tracing, the middle that of the Time, the lower that of the Blood-pressure manometer

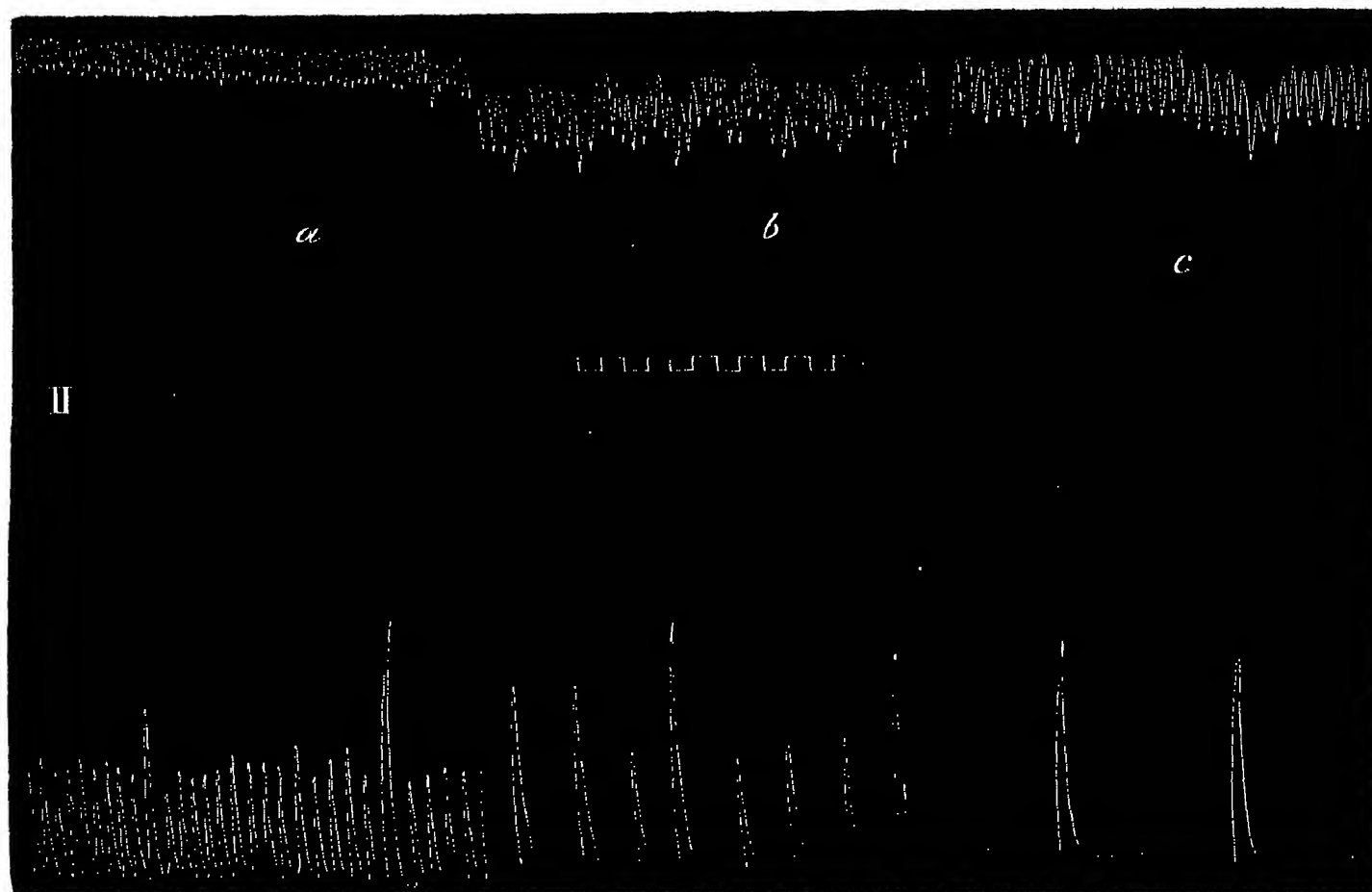
A (1) For circumstances, *vide supra*.

V. Changes in the height of the blood pressure, and the abnormal development of the respiratory variations in the blood pressure.

*α.* At first these variations are very slightly marked, even with the deep inspirations. As the pressure increases the variations are produced, and the curves grow longer as the respirations become slower (see Tracing II.).



## Tracing II



The upper line is the tracing of the Blood-pressure, the middle that of the Time, and the lower that of the Respiration.

$\beta$ . Vasomotor curves appearing and growing longer with the increasing pressure.

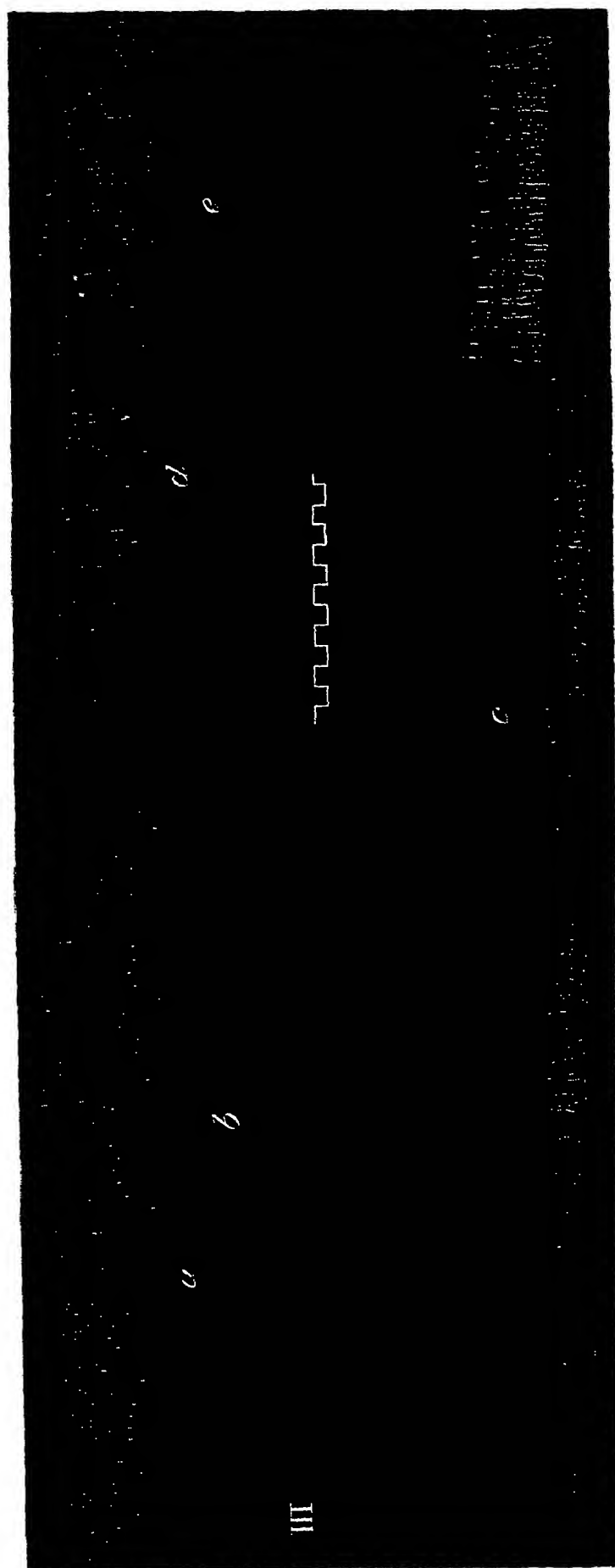
At the beginning there are none, the pressure being insufficient. But on the application of more pressure they appear, then tend to get less distinct. Additional pressure produces them again, but the curve is longer. After all pressure has been removed the curves are not seen. These phenomena are independent of the respiration and of the rate of the heart (see Tracing III.).

$\gamma$ . Slight primary rise of blood pressure.

A preliminary rise of the blood pressure is never well marked in the Dog, and is only produced by putting on an adequate pressure suddenly. In the Tracing IV. this was done at the points marked 300.

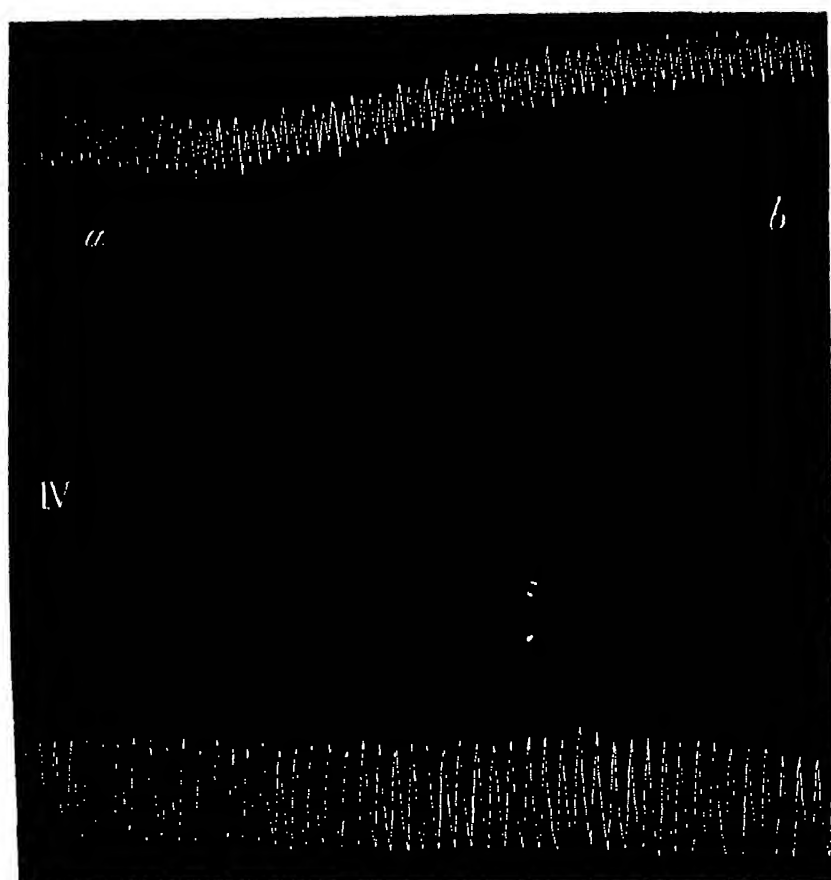
In the Monkey this phenomenon of a primary rise instead of the usual fall is well marked, see Tracing V., but it would appear to be due to some pressor influence which is easily lost. Thus on repeating the application of pressure there may be no rise. In the tracing after the recovery from the first application, exactly the same pressure was again used, but here resulted the customary fall in the blood pressure instead of the rise first observed (see Tracing VI, taken from the same experiment).

Tracing III



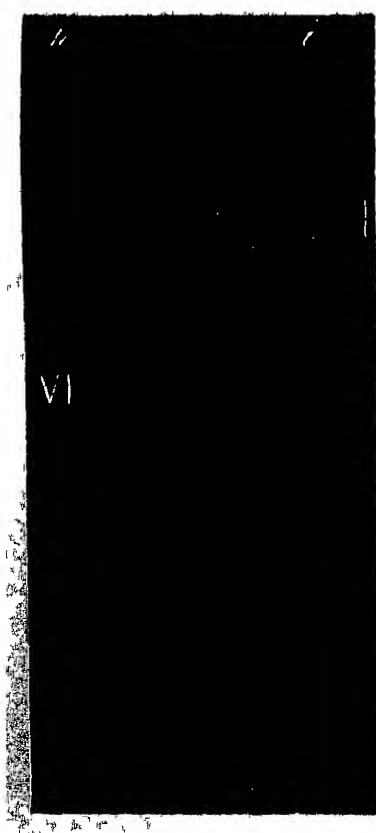
The upper line is the tracing of the Blood-pressure, the middle that of the Time, and the lower that of the Respiration

Tracing IV



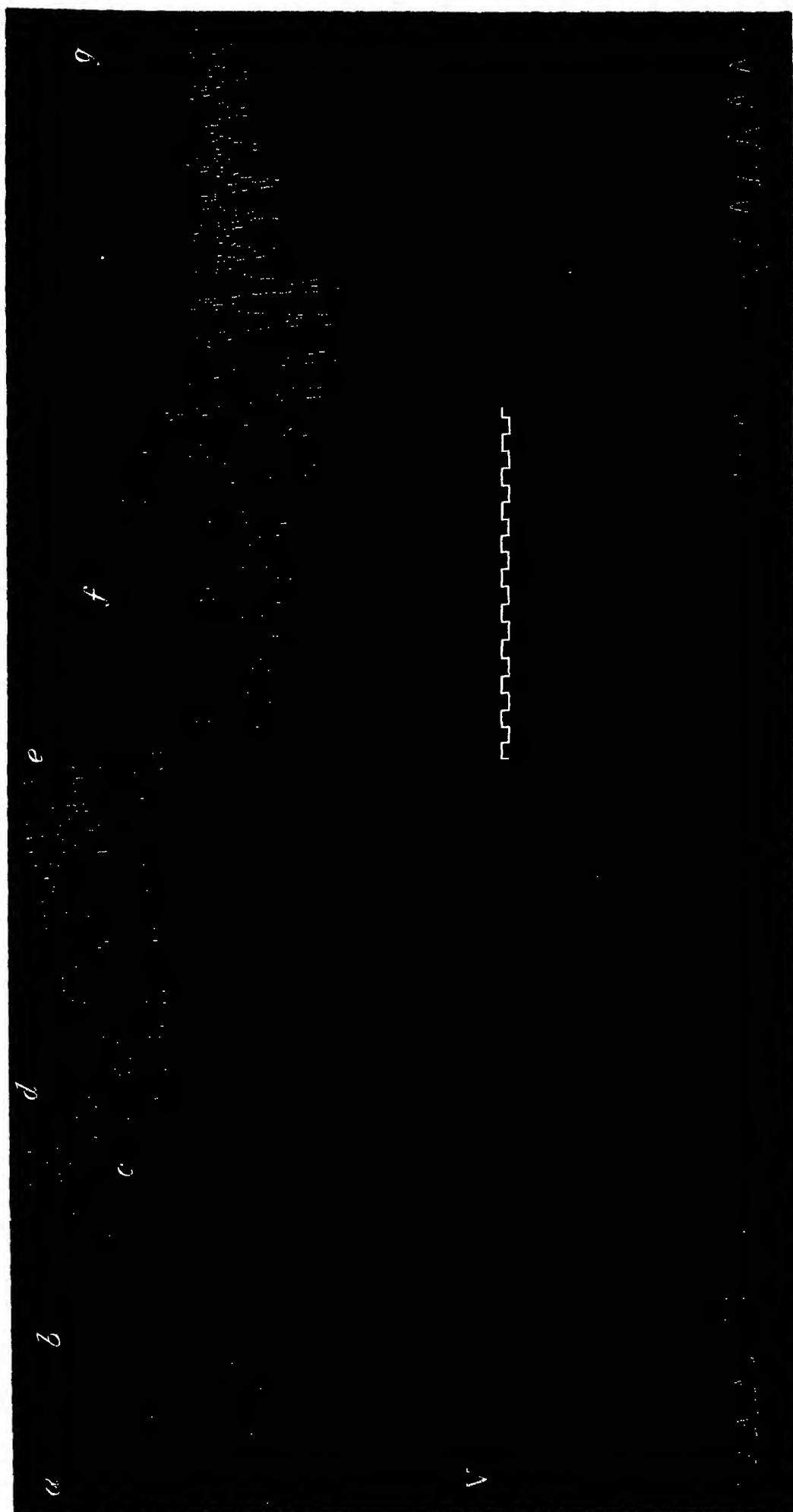
The upper line is the tracing of the Blood-pressure, the lower that of the Respiration

Tracing VI



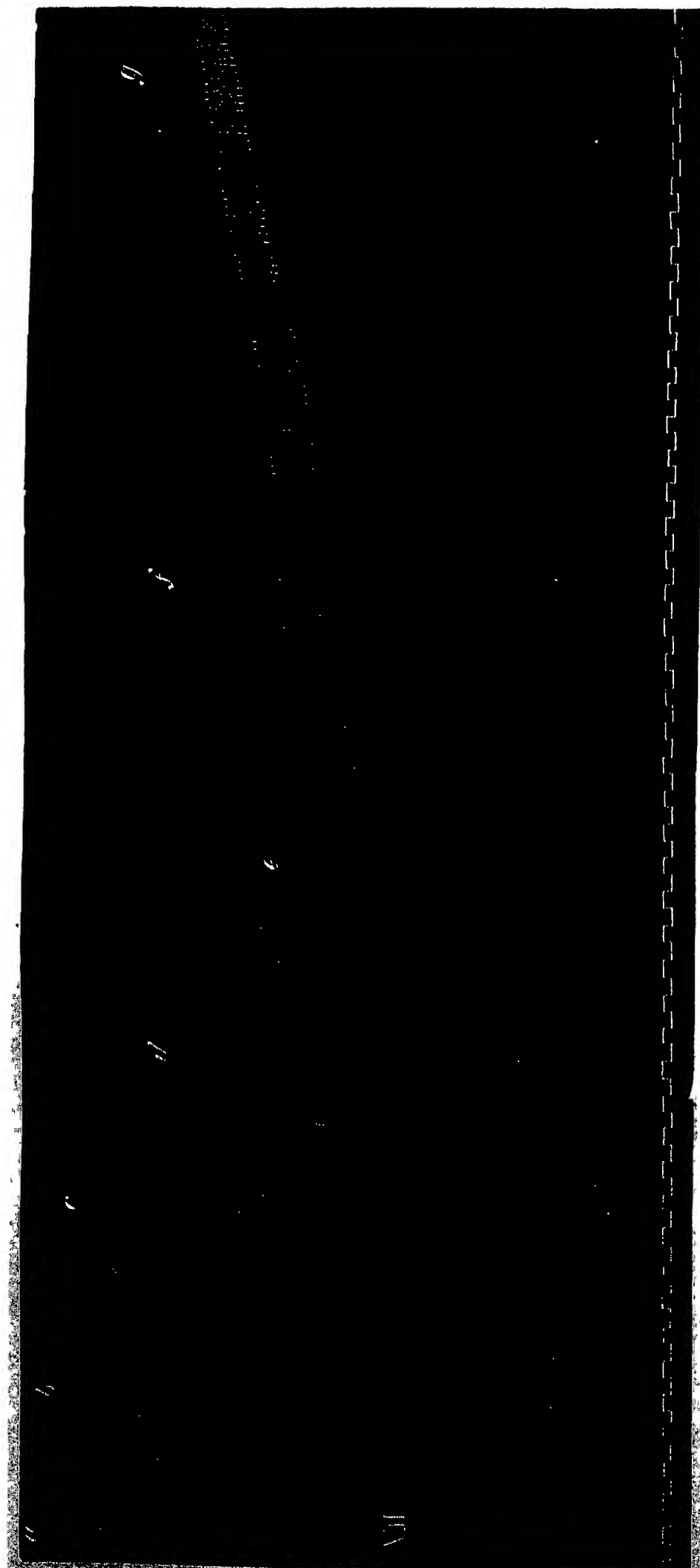
The upper line is the tracing of the Blood-pressure, the middle that of the Respiration, the lower that of the Time.

Tracing V



The upper line is the tracing of the Blood-pressure, the middle that of the Time, the lower that of the Respiration

Tracing VII



The upper line is the tracing of the Blood-pressure, the middle that of the Respiration, and the lower that of the Time

### δ Fall of blood pressure

The blood pressure usually falls slightly before the heart rate is slowed. In some cases this depressor effect is very marked and apparently persists (see Tracing VII). For, after the vagi had been divided, the rise in blood pressure was only very slow, differing much from the sudden rise which usually takes place on that operation. The phenomenon usually only occurs with the first application of the pressure, *vide infra*. This active depressor influence also occurred with an arrest of respiration, and the respiration did not begin again for some time after the pressure had been removed, and artificial respiration had been used. The connexion of these two facts will appear under B.

A (1) R. For the effects upon respiration see A. (2), the effects in the present section being so slightly marked.

A (2) H. *Slowing, arrest, and recovery of heart.*—When pressure is applied to any part of the cerebral or cerebellar hemispheres.

α. Slowing and arrest of the heart preceded by cessation of the respiration. The respiration ceases, the heart which before was going at a normal rate is immediately slowed and is soon arrested. In such a case the effect of artificial respiration is such that the action of the heart immediately recommences, and the rhythm becomes of its former rate although the pressure is still applied, *vide β prox*.

β. Slowing increased, and arrest produced, preceded by the cessation of respiration.

In Tracing VIII. the heart on recovery is found to be still slowed.

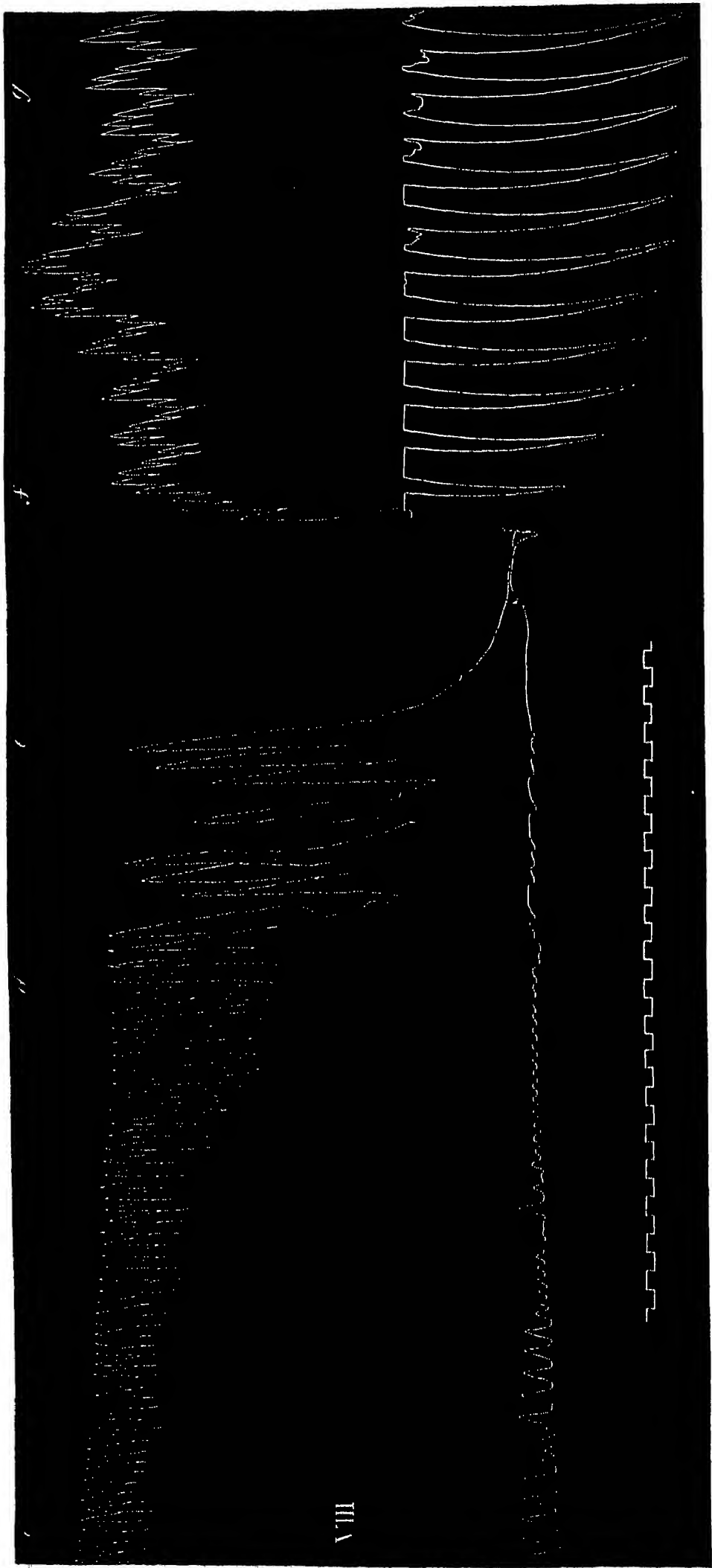
γ. Slowing of heart with arrest of the respiration, persistence of both effects after the pressure was taken off.

The heart is slowed, and the more markedly as the arrest of respiration is reached. If the pressure be removed before the slowing has led to an arrest, the heart does not immediately quicken, but remains for several beats slow. If the natural respiration then commence the heart gradually reverts to its former rate. For example see end of Tracing V.

δ. Arrest of the slowed heart occurring after the pressure has been taken off, and persisting in the presence of respiration, natural or artificial. This is shown in Tracing IX.

It will be seen that the blood pressure had shown a slight tendency to rise when the heart was arrested suddenly. The latter began again with artificial respiration.

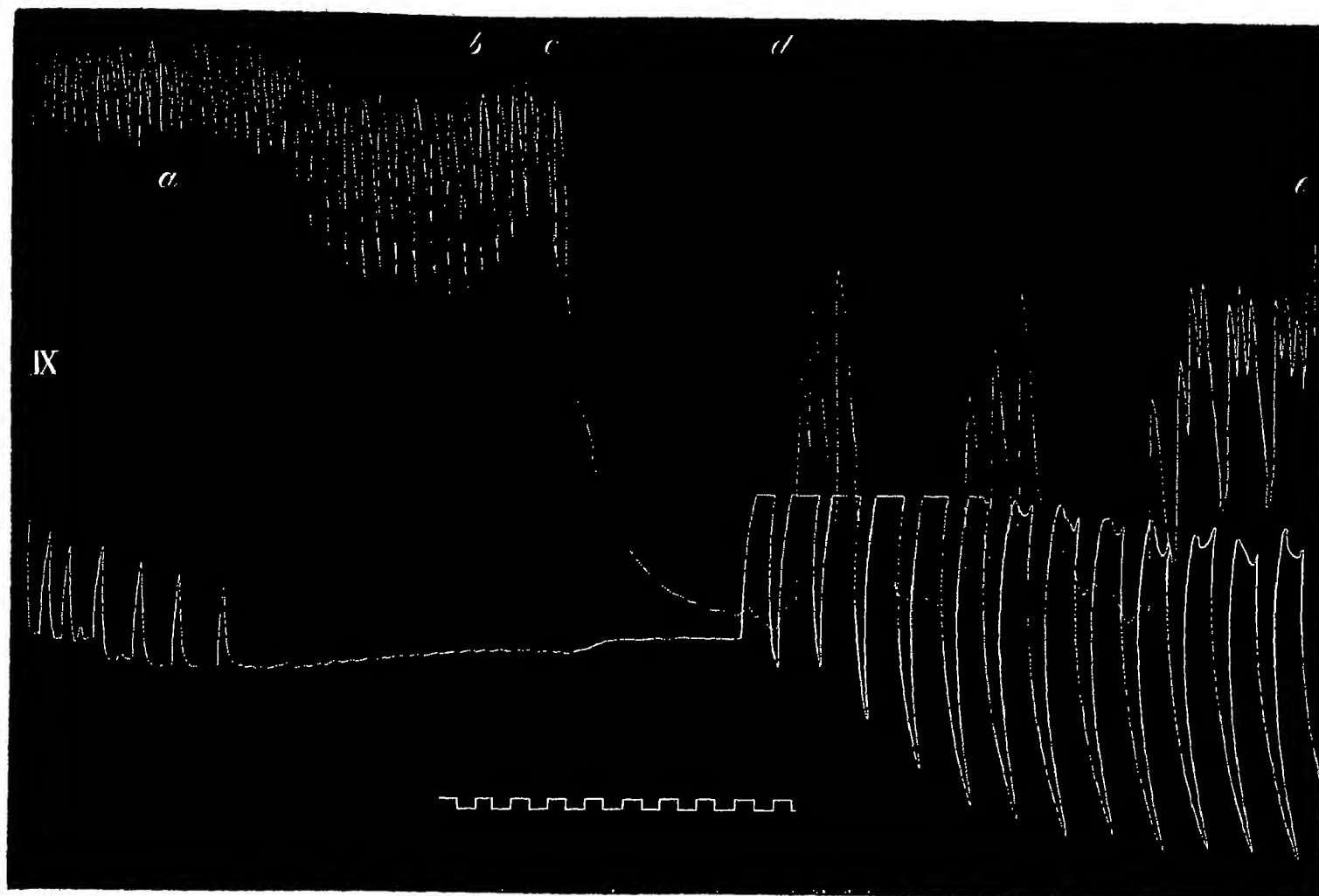
Tracing V



The upper e he o he Blood-p e, the ddle hat of the Respiration and the lower that of the Time



## Tracing IX



The upper line is the tracing of the Blood-pressure, the middle that of the Respiration, and the lower that of the Time

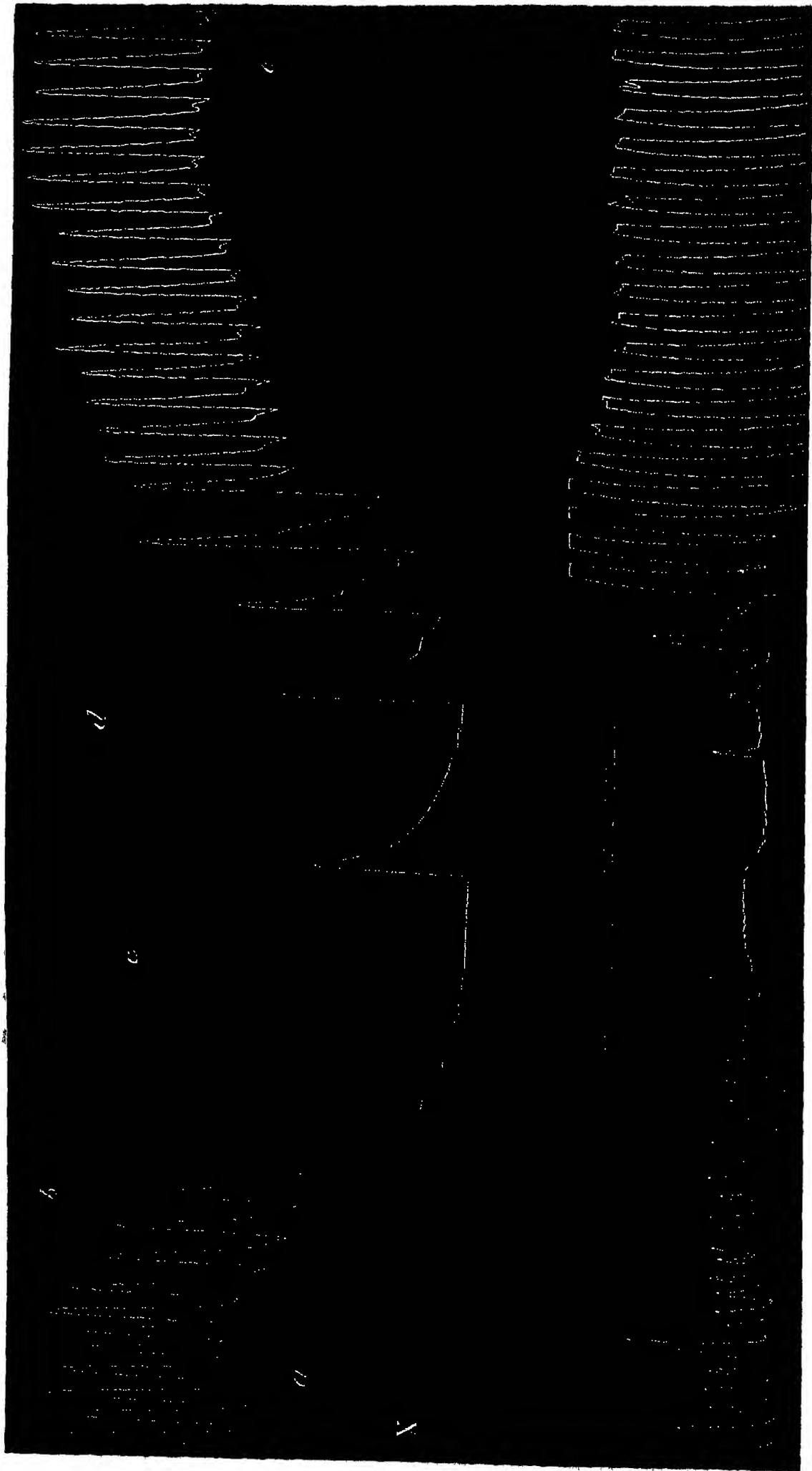
ε Slowing and arrest of the heart ; re-starting, and continuing slow.

In this case the heart was slightly, then greatly slowed, then arrested. Its arrest took place before the respiration, and continued for some time, in spite of the employment of artificial respiration. When the heart started it was at a very slow rate, and it persisted at the slow rate for a long time, during which the artificial respiration continued (see Tracing X.).

ζ Slowing and arrest of the heart during artificial respiration, arrest continued for a long time after taking off the pressure. As seen in Tracing XI the rate of the heart in this state became much slower, and was then suddenly arrested. It did not start again, although the pressure was taken off. Meanwhile only the weak cardiac waves excited by inflation, &c., of the thorax, caused by the artificial respiration, were to be seen in the manometer tracing (see also Tracing XII.).

After some time the heart began again, but it continued slow for a long while. Afterwards it gradually became quicker, and the artificial respirations were then

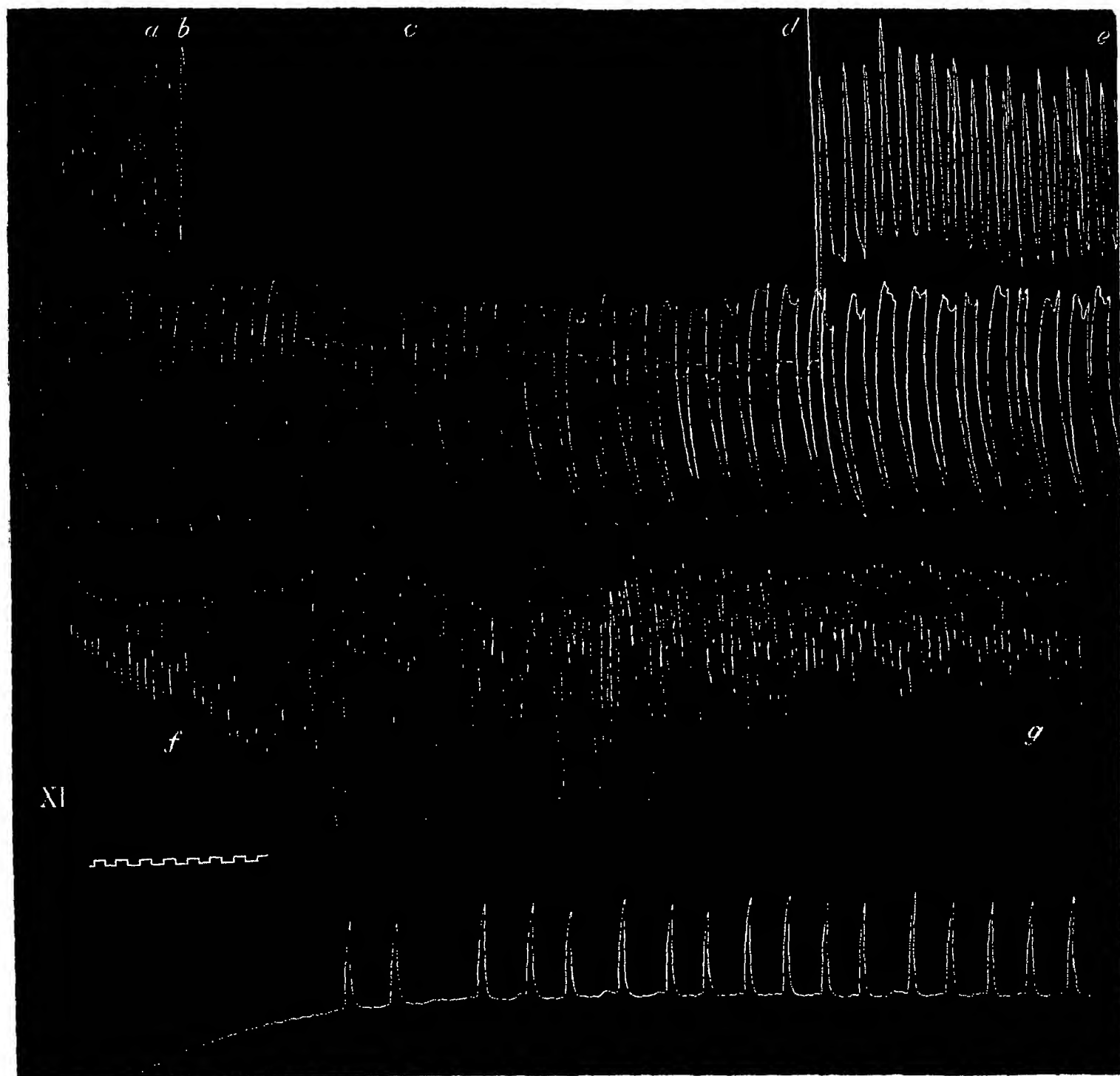
Tracing X.



The upper line is the tracing of the Blood-pressure, the middle that of the Time, the lower that of the Respiration

stopped The rate again became slow, but when natural respiration began the heart rate continued to increase.

## Tracing XI



The upper line is the tracing of the Blood-pressure which is continued in the third line, the second line is that of the Respiration which is continued in the fifth line, the fourth line is the tracing of the Time.

$\eta$  Arrest of heart immediately on application of pressure, and without previous slowing

This was only obtained purely when the bag was put into the fourth ventricle, *vide* p. 239, since with pressure applied in other places more or less slowing took place first (see Tracing XXIII.).

*θ* Arrest of heart, with or without previous slowing, not starting again

This is likely to take place when pressure is applied in the fourth ventricle, and it may happen from sudden severe pressure in other parts of the brain. Generally, however, recovery is brought about by resorting to artificial respiration.

*ι* Arrest of the heart, starting again by forcible beats, separated by long intervals

This condition of the heart's action is sometimes remarkably pronounced, as is seen in Tracing XII. After the arrest artificial respiration called forth only one beat. Next three were produced by perfusing fluid through the cannula. The heart began with large beats, separated by wide intervals. As a mode of recovery this is interesting.

*κ* Increased rapidity of the heart after being slowed, the rapidity being as great as after division of the vagi, and probably due to failure of the vagal centre (see Tracing XIII.). At the left-hand side is seen the slow cardiac rate due to the pressure; the rhythm is then seen gradually increasing in rate, until it becomes fully three times as fast, the pressure being maintained all the time. Concomitantly with the increase in rate is a rise in the blood pressure.

This condition of the vagal apparatus may (as seen in the tracing) be recovered from.

A further proof is shown in Tracing XIV., where we found that when this dissolution of the vagal centre was thus effected, subsequent division of the vagi, as might be expected, produced no change in the condition.

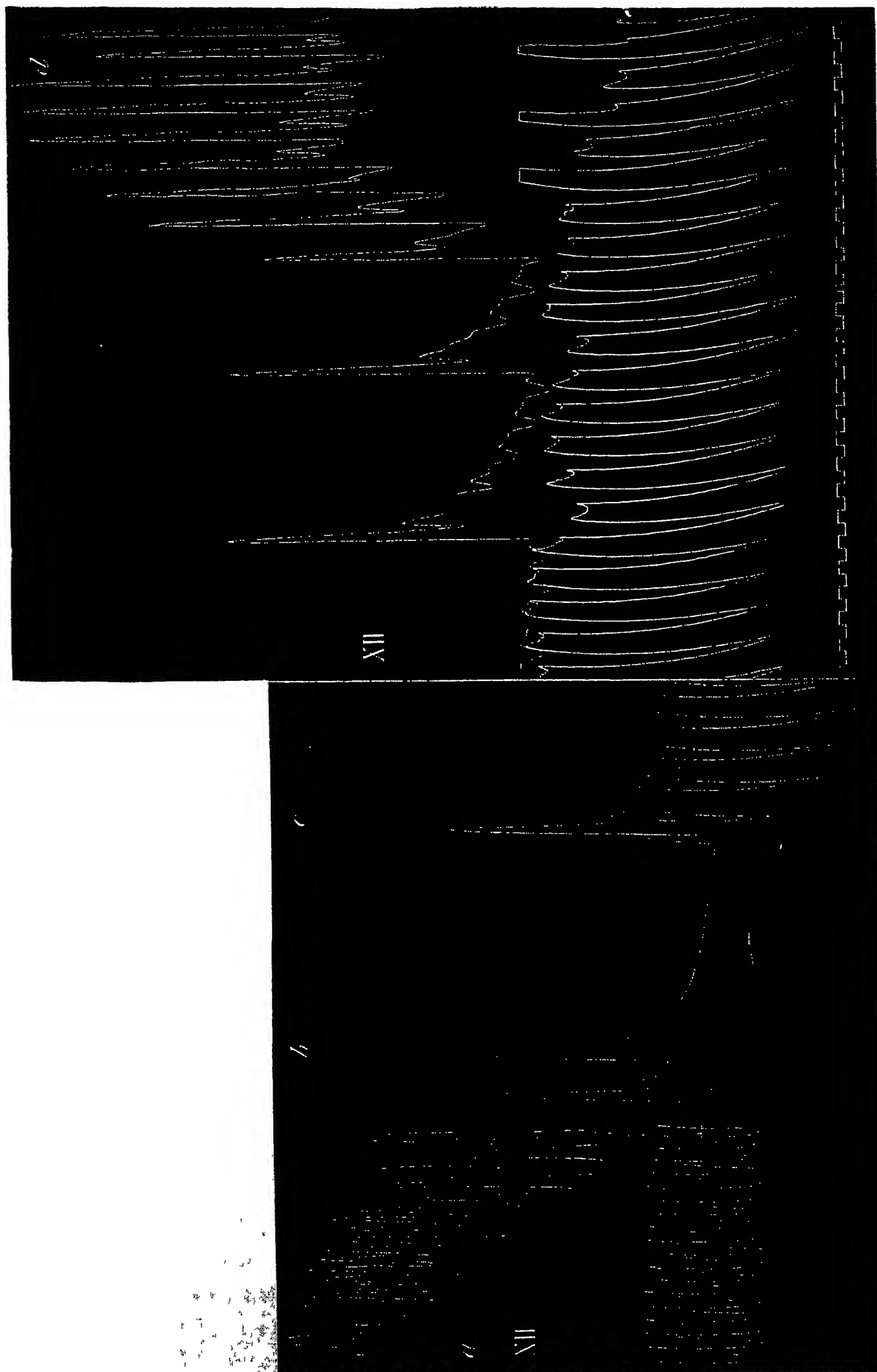
*λ* Intermision in extent of heart beat

This usually occurred when arrest was impending during maintenance of the pressure, but often persisted after the pressure had been removed, sometimes appeared temporarily during recovery from the effects of the pressure, or continued after the respiratory rhythm was perfectly re-established.

The rate of intermission varied from the second to the sixth beat in different cases, and had a notable tendency to fall into time with the respiratory rhythm.

We now proceed to discuss the vasomotor phenomena (V) observed under these conditions.

Tracing XII.

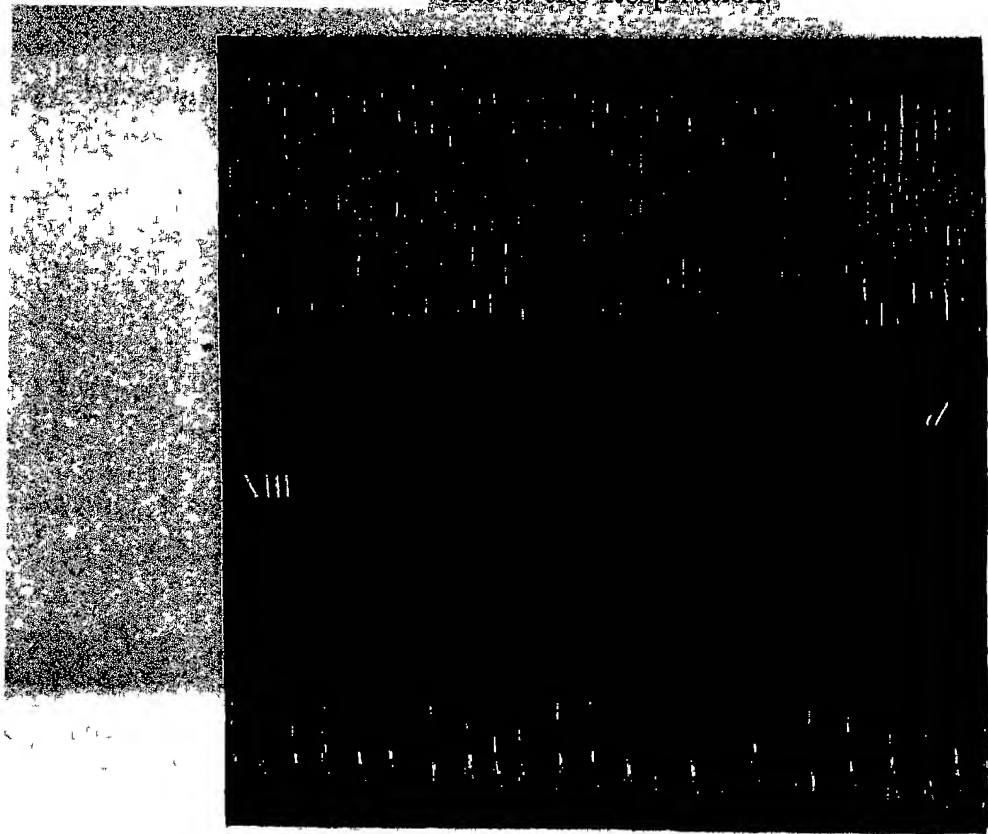


The upper line is the tracing of the Blood-pressure, the middle that of the Respiration, and the lower that of the Time

Tracing XIII

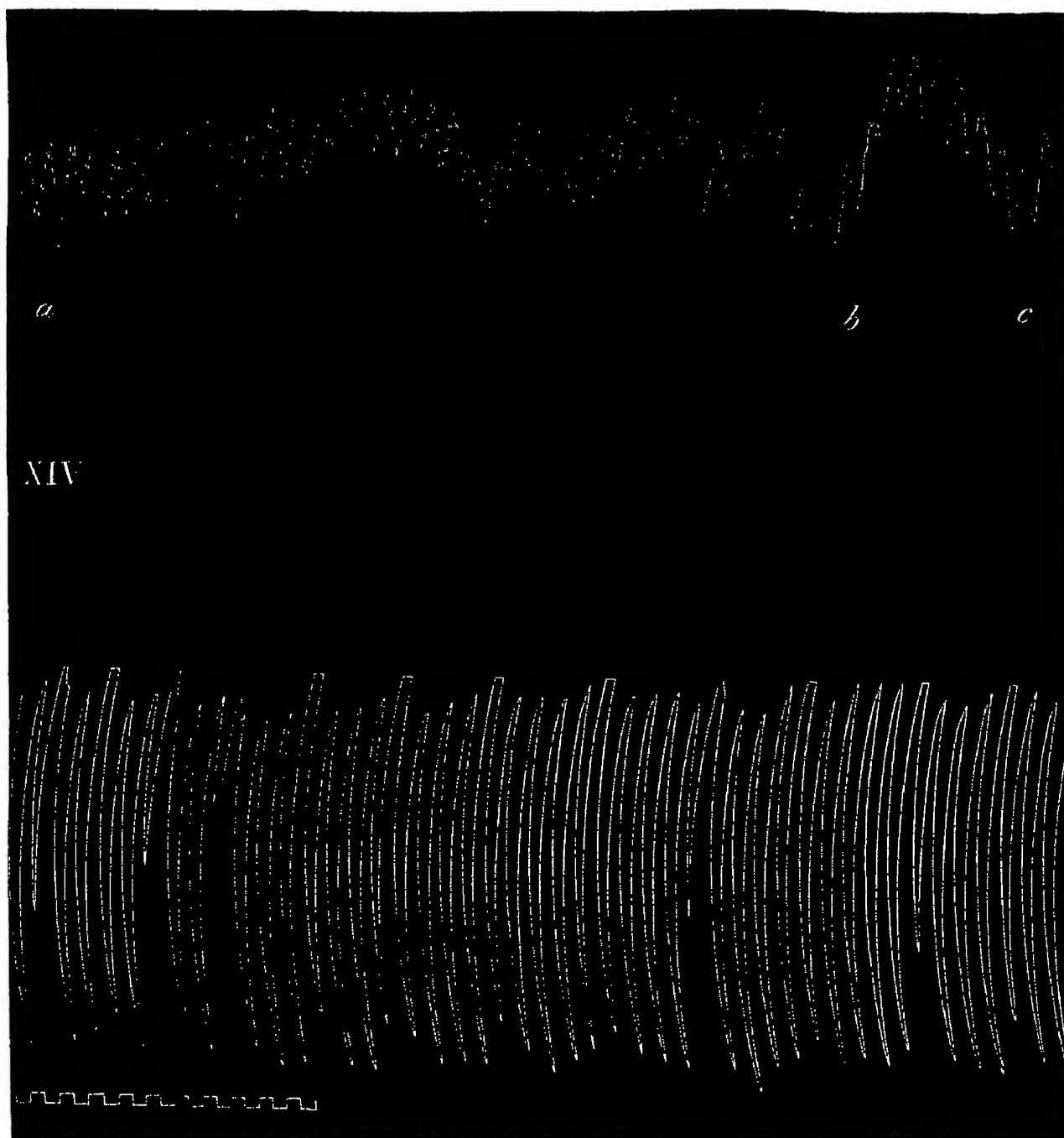


The upper line is the tracing of the Blood-pressure, the second and fourth that of the Time, the third that of the Respiration.



The upper line is the tracing of the Blood-pressure, the lower that of the Respiration

## Tracing XIV



The upper line is the tracing of the Blood-pressure, the middle that of the Respiration, the lower that of the Time

A *Pressure applied to any part of the brain*

(2) *Slowing and arrest of heart*

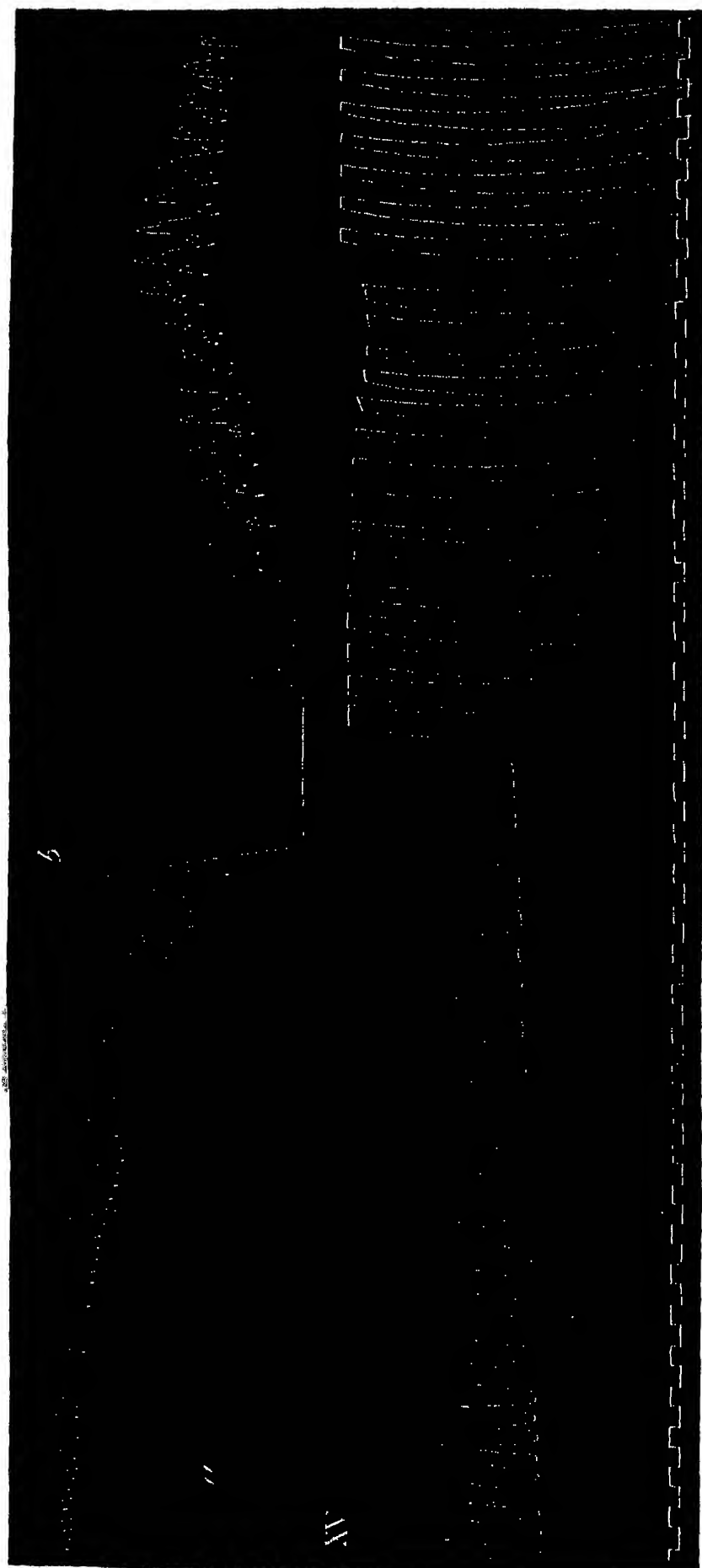
V a. Fall of blood pressure preceding the slowing of the heart, and continuing after recovery of the rhythmic heart rate.

In the instance shown in Tracing XV. active depressor influences caused a fall of the blood pressure before the arrest of the heart. After the return from zero the blood pressure continued low

The same phenomenon could also be observed to continue even after section of the vagi (see Tracing VII.)

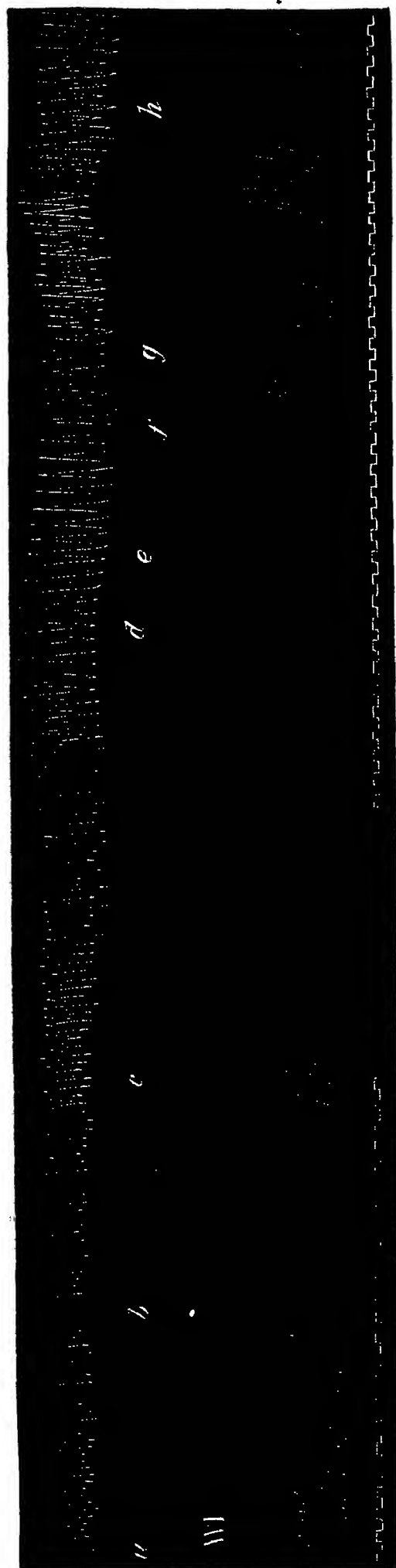


Tracing XV



The upper line is the tracing of the Blood-pressure, the middle that of the Respiration, and the lower that of the Time.

Tracing XVI



The upper line is the tracing of the Blood-pressure, the middle that of the Respiration, the lower that of the Time

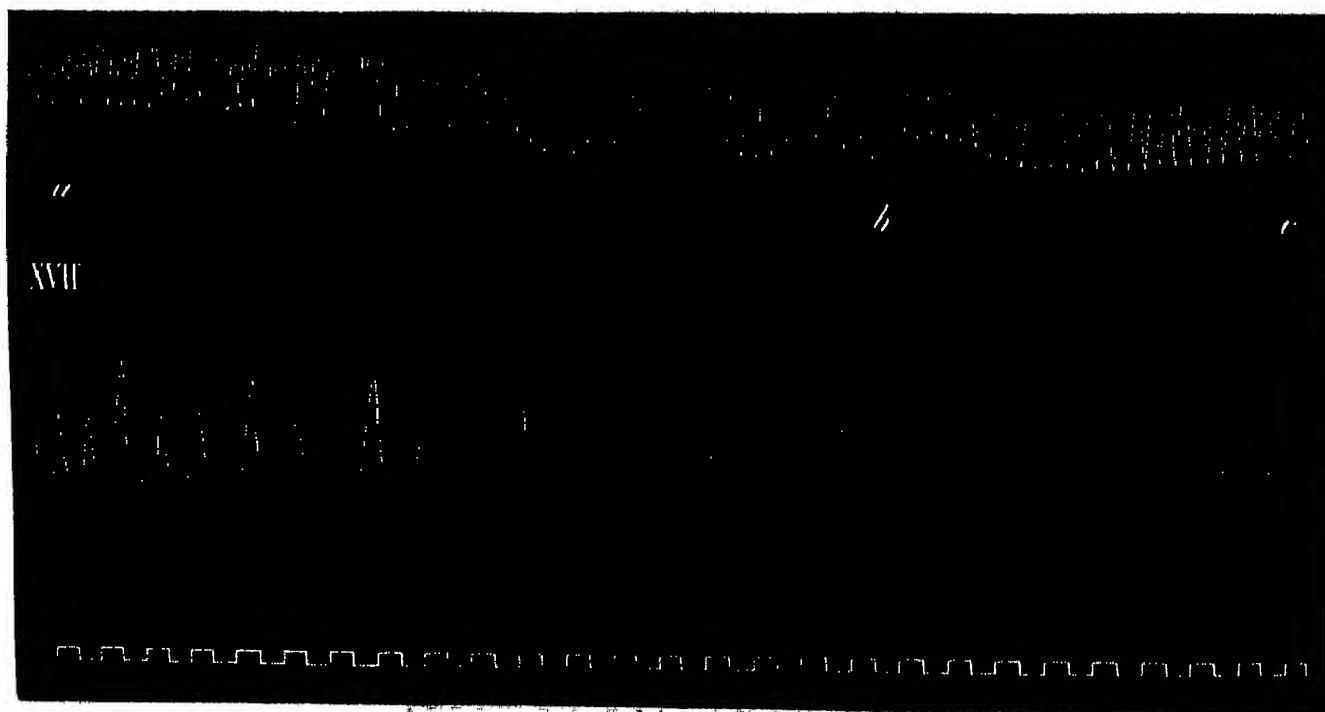
$\beta$  Depressor influences absent, although the pressure was applied for the first time, and also absent after the arrest of respiration

This almost inexplicable fact was observed once, as seen in Tracing XVI. It is seen that, although the heart became gradually slowed down to 35 per minute, there was no fall of blood pressure. This absence of depressor influence may have been connected with the low blood pressure. That vasomotor phenomena, *e.g.*, curves, could yet be produced is seen in the tracing at *a*, where it is shown that the pressure developed vasomotor curves which continued for some time and then disappeared when the heart was slowed.

$\gamma$  Depressor influences absent when pressure was applied for the second time, after having been present on the first application.

In harmony with the foregoing this depressor influence we found to be easily destroyed in the course of an experiment, since it usually disappeared after the brain had been once compressed (see Tracing XVII.)

Tracing XVII.



The upper line is the Tracing of the Blood-pressure, the middle that of the Respiration, the lower that of the Time.

In a well-marked case the heart was only slightly slowed even after the arrest of respiration, and there was no fall of the blood pressure. This loss of depressor influence is further indicated by the blood pressure being actually above that existing before the beginning of the experiment.

In other cases the heart could be and was greatly slowed without any fall of blood

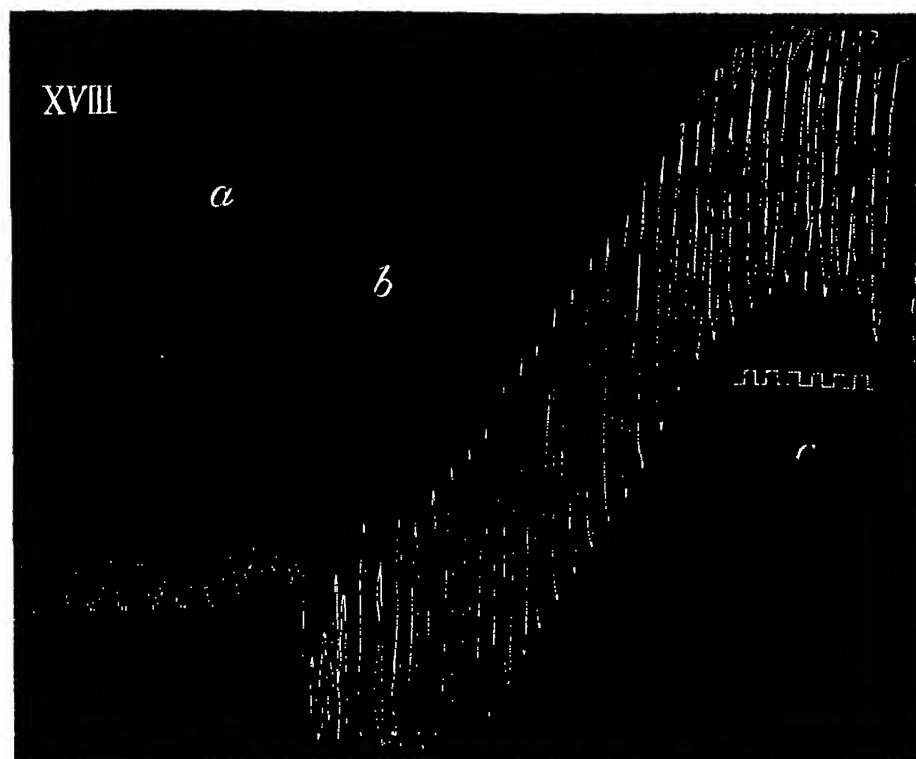
pressure, if the depressor influence had been lost during the previous application of pressure

- δ Pressor influences causing a rise to the level attained before the application of pressure, or even somewhat higher, the heart remaining slower than usual or returning to its normal rate.

For the development of this effect (see Tracings VIII, X) it was usually necessary to employ artificial respiration to recover the action of the heart. That it is a true vasal effect is well seen at the end of Tracing X, where the rise of pressure is obtained and maintained, although the extent of each heart beat is no greater than before

- ε. Pressor influences causing a rise considerably above the normal level, attended by either a quickening of the previously slow heart beat or by maintenance of the same slow rhythm. This is seen in Tracings XVIII, XII, XIII

Tracing XVIII



One line is the Tracing of the Blood-pressure, the other of the Time

- ζ Pressor effect equal to that appearing after division of the vagi and attended by a heart rate of a similar character

We have already shown that the heart rate under certain circumstances of intra-cranial pressure gives evidence of the failure of the bulbar vagus centre. As is shown in Tracings XIII, XIV., this is also true of the vasomotor condition which is customarily produced by section of the vagi, plus an increase of the intra-cranial tension.

η Vasomotor curves appearing after the application of pressure.

Whereas prolonged or severe pressure abolished both respiratory and vasomotor curves, normally superadded on the manometric tracing, slight pressure occasionally *developed* vasomotor curves as is seen in Tracing XVI

As the heart rate quickens after the temporary slowing, respiratory curves appear on the tracing, usually exaggerated at first and subsequently becoming of normal extent (See Tracing V)

A (2) R Changes in respiration when the intra-cranial pressure is applied to any part of the encephalon, and when such pressure produces slowing and arrest of the heart's rhythm

It will be remembered that on p 219 we stated that the changes in respiration which accompanied only slight alteration (slowing) of the heart rate were so precisely similar to those which preceded complete arrest of the heart that we would consider them *en bloc*

We must here allude to certain side issues connected with our method before entering upon the task of classifying and collating the results obtained

The recording apparatus, as before stated, gave us the movements of the thoracic walls only, the ascent of the curve marking a natural inspiration or an artificial inflation of the chest. Our tracings consequently give variations in the depth of the movements of inspiration and expiration, as well as changes in the rhythm. We, however, also employed on many occasions artificial respiration; this, especially after the observations of HERING and BREUER,\* is well known to notably affect the respiratory centre in the medulla oblongata. We would propose, therefore, in view of these facts, to arrange the results as follows:—

Class I.	Changes in respiration uncomplicated by artificial respiration	(a) Changes in rhythm . . .	<div> <div>Inspiration</div> <div>Expiration</div> <div>Pause</div> </div>
		(b) Concomitant changes in rhythm and extent	<div> <div>Inspiration</div> <div>Expiration</div> <div>Pause</div> </div>
		(c.) Changes in extent . . .	<div> <div>Inspiration</div> <div>Expiration</div> <div>Both</div> </div>

Class II Mode of natural recovery of changes in respiration.

Class III. Changes in respiration Recovery as observed after the employment of artificial respiration.

\* See p 234

## Class I Changes in respiration uncomplicated by artificial respiration

(a) *Changes in Rhythm*—The change in rhythm is gradual, slowing as the effect of the pressure becomes more marked. The pauses become lengthened, and, as will be seen in Tracings II, XV, XVII, inspiration is deepened. If the degree of anæsthesia were light there were —

(b.) *Concomitant Changes in Rhythm and Extent*.—When the rhythm is slowed as a rule the extent of the respiratory movements becomes for the time increased, but just before arrest they become shallow (*Vide infra*)

(c) *Changes in Extent*—The condition just alluded to is really so dependent upon the development of inspiration that it is best further considered under the head of change in extent

On the whole the usual early effect is as a rule increase of inspiration. This inspiratory increase generally shows itself in one of two ways. Either—

(1) By deep single inspirations occurring at fairly regular intervals. (See Tracing II)

(2) By an inspiratory spasm, in which it is usually seen that both expiratory and inspiratory movements have for some time been diminishing, but that just before the final arrest, expiration seems to fail, and so an inspiratory spasm is produced. (See Tracing XVI) This spasm only lasts three or four respiratory intervals, and is followed usually by a few small double respiratory movements and then complete arrest occurs

We can look upon this phenomenon in another way, viz, that the dissolution of the respiratory centre is signalled by failure of expiration, and so has brought about undue predominance of inspiration. In this way the influence of the pressure would not necessarily mean exaggeration of inspiration, but merely over-action in consequence of the disappearance of the antagonistic expiration. This view is suggested to us by the investigation of RICHET\* upon the dissolution of respiration effected by anæsthetics, he having shown that active expiration disappeared long before inspiration

## Class II. Mode of natural recovery of respiration

The effect of the increase of pressure has been just described, it now remains to discuss the manner in which the respiratory centre begins to recover its function unaided by artificial respiration.

Rarely the respiratory movements have continued although extremely reduced in extent

After the more usual complete arrest respiration very frequently recommences by an initial deep inspiration, and this is followed by another (gasps in fact), then successive respirations follow in increasing order of depth. (See Tracing I)

\* 'Mémoires de la Société de Biologie,' 1887, p. 25.

In fewer instances the respirations recommence not as gasps, but simply as shallow movements increasing in extent

### Class III Changes in respiration observed after the employment of artificial respiration

The effect of artificial respiration has usually been observed when the latter has been employed to obviate fatal results of severe pressure, consequently in every case the respiratory centre is being, or has been inhibited by pressure

Two points call for consideration at this juncture, firstly the general improvement in the activity of the centre produced by the increased oxygenation of the blood, and, secondly, the direct inspiratory and expiratory stimuli evoked by the suction and distension respectively of the lung \*

The effects observed have been roughly divided into two categories, one in which apnoea occurred and another in which it was absent

When apnoea followed, the respiratory movements usually commenced again, having a good depth, but when no apnoea was produced, *i.e.*, when the respirations almost immediately recommenced, the movements were shallow. This difference, however, is not to be regarded as in any way absolute.

Before passing on to the next chapter, *viz.*, the variation in the foregoing results produced by section of the vagi, we must offer a few further remarks on the abolition of the respiratory function, especially as regards its parallelism with the arrest of the heart.

Of the two, respiration is almost invariably affected first, *i.e.*, in rhythm and extent. The arrest of respiration, however, ought not to be regarded as strictly comparable to the condition of arrest of the heart, since the latter implies excitation of a bulbar centre, whereas arrest of respiration means paralysis, *i.e.*, an effect of much greater importance

Hence the fact that the two are arrested simultaneously (see Tracing XXIII.), or even the respiration a little after the heart (see Tracing X.), only goes to show that the respiratory centre is by far the more sensitive; and consequently, as an index of pressure, more delicate than the heart's action.

#### A (3.) The variation in the effects observed to be produced by section of the vagi.

We have made a large number of observations after preliminary section of the vagi. The effect of division of one vagus was practically nil.† When it was pulled on

\* HERRING and BREUER "Die Selbststeuerung der Athmung durch den Nervus Vagus." 'Sitzber. d. K. Akad. d. Wissenschaft'; Wien, 1868, April, November (vol 57, *Abth.* 2, p 672, vol. 58, *Abth.* 2, p. 909) See also HEAD, 'Journ of Physiology,' 1889, and other authors.

† We did not make special observations on this point, except to satisfy ourselves that the heart could be slowed through one vagus nerve by increased intra-cranial pressure.



slightly for the purpose of division the tension produced a temporary slowing of the heart

Division of both vagi invariably produced the classical phenomena of—

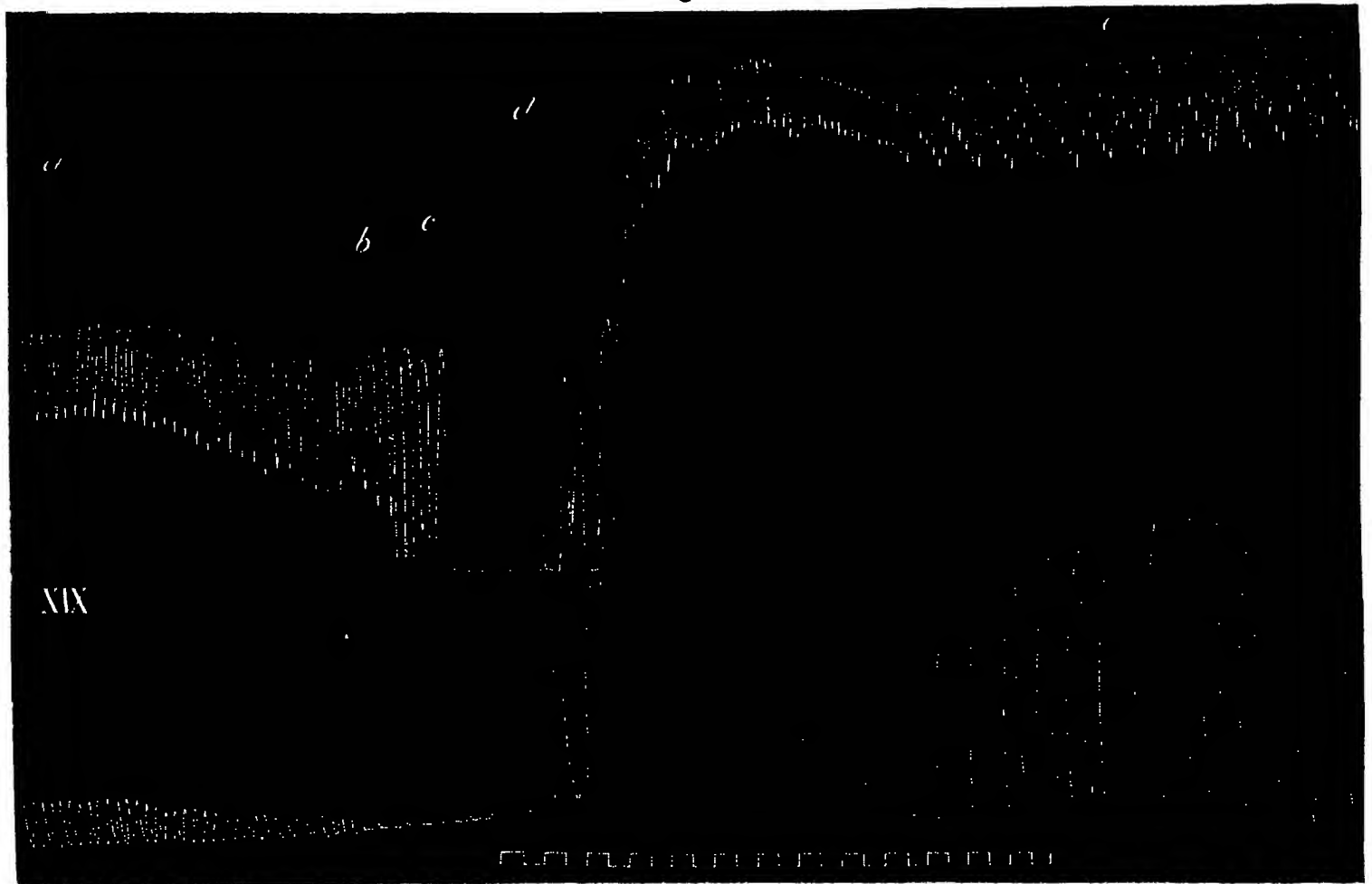
- (1 ) Rapid heart action.
- (2 ) Rise of blood pressure
- (3 ) Alteration of respiration

Following Leyden\* it was obviously of extreme importance that these variations should be studied under the condition of increased intra-cranial pressure.

We therefore prepared the vagi in the usual way and divided the nerves, sometimes before pressure was applied, sometimes while it was acting

The general results remained the same

Tracing XIX.



The upper line is the tracing of the Blood-pressure, the middle that of the Respiration, the lower that of the Time

A (3.) H. After division of the vagi the heart rate immediately became rapid and was unaltered by increase of the intra-cranial pressure, but when the latter caused a rise of blood pressure the rate was notably quickened, slowing again as the blood pressure fell

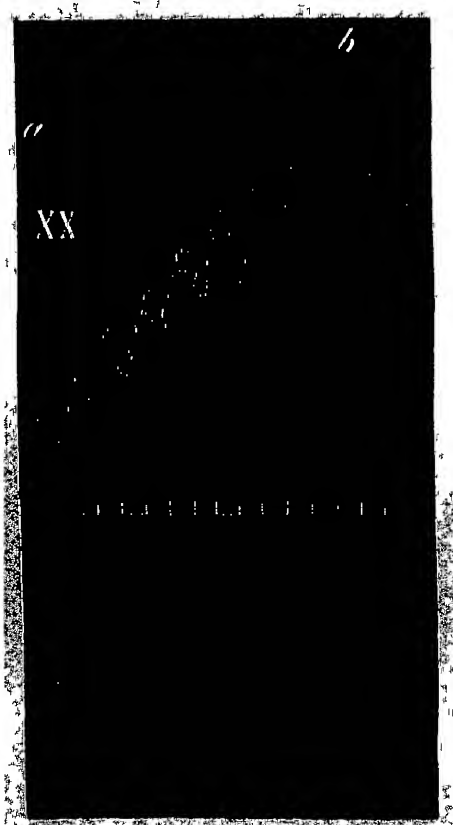
\* *Loc cit*

The effect on the heart is thus of minor importance, but as will be now seen, the change in the blood pressure evoked by rise of the intra-cranial pressure after division of the vagi is most remarkable (*Vide* also Historical Introduction, BERGMANN)

A (3) V Firstly it is to be noted that, after a depressor influence has been occasioned by raising the intra-cranial pressure, the effect of dividing the vagi is only to slowly develop the remarkable additional rise in the blood pressure. (*Vide* Tracing VII)

With this preliminary notice of possible depressor effect we must proceed to describe the pressor influence, which is so eminently characteristic when the intra-cranial pressure is raised. It is sufficient perhaps to state that after division of the vagi the effect of putting on pressure is to immediately cause a rapid rise in the blood pressure. So long as the vasomotor central apparatus is intact and in functional activity, this rise continues to advance with additional increase of pressure until the extreme point now to be mentioned is reached.

Tracing XX.



The upper line is the tracing of the Blood-pressure, the middle that of the Time, and the lower that of the Respiration.

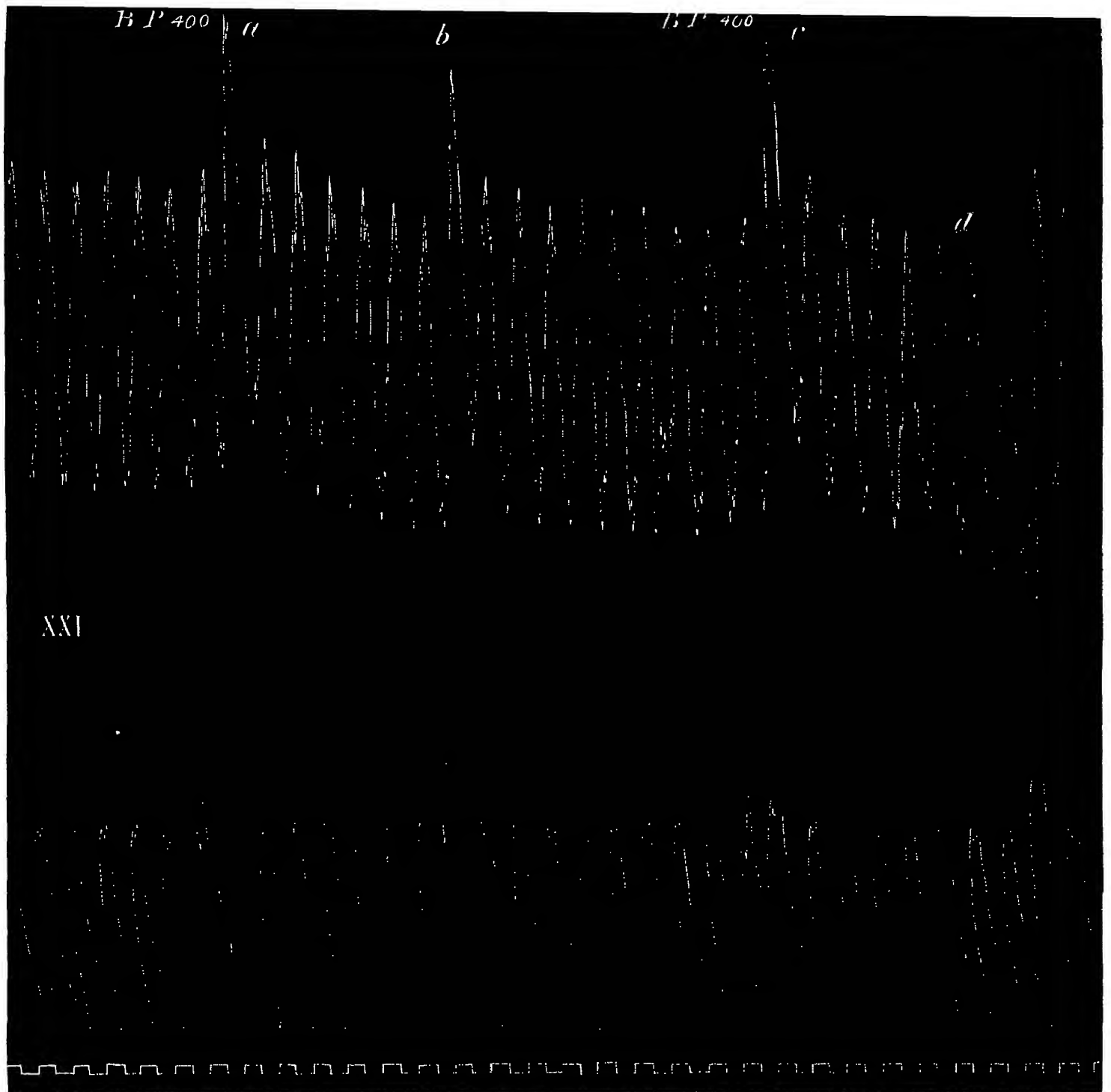
This point may be even as high as 300 mm. Hg, i.e., about twice the blood pressure of a large normal Dog.

A still further rise of the blood pressure can be produced by starting artificial respiration, and so improving the condition of the vasomotor centres. (See Tracing XX.)

Finally, an extremely high blood pressure, e.g., actually 400 mm. Hg, can be obtained in the following manner.—

The vagi having been divided while the blood pressure is good (*i e*, 130 mm Hg), and the intra-cranial pressure raised, but not so severely as to arrest respiration, the blood pressure will, in accordance with what has just been said, be found to have risen to nearly 300 mm. Hg. If now artificial respiration be commenced and the

Tracing XXI.



The upper line is the tracing of the Blood-pressure, the middle that of the Respiration, the lower that of the Time

intra-cranial pressure increased, it will be found that the blood pressure will continue to rise to about 340–360 mm, and then while at this great height it will rise to even 400 mm. if a natural inspiratory impulse happen to coincide with the commencement of an artificial expiration (See Tracing XXI)

As the vasomotor centre begins to fail under the continued pressure, this effect begins to fall off and finally disappears

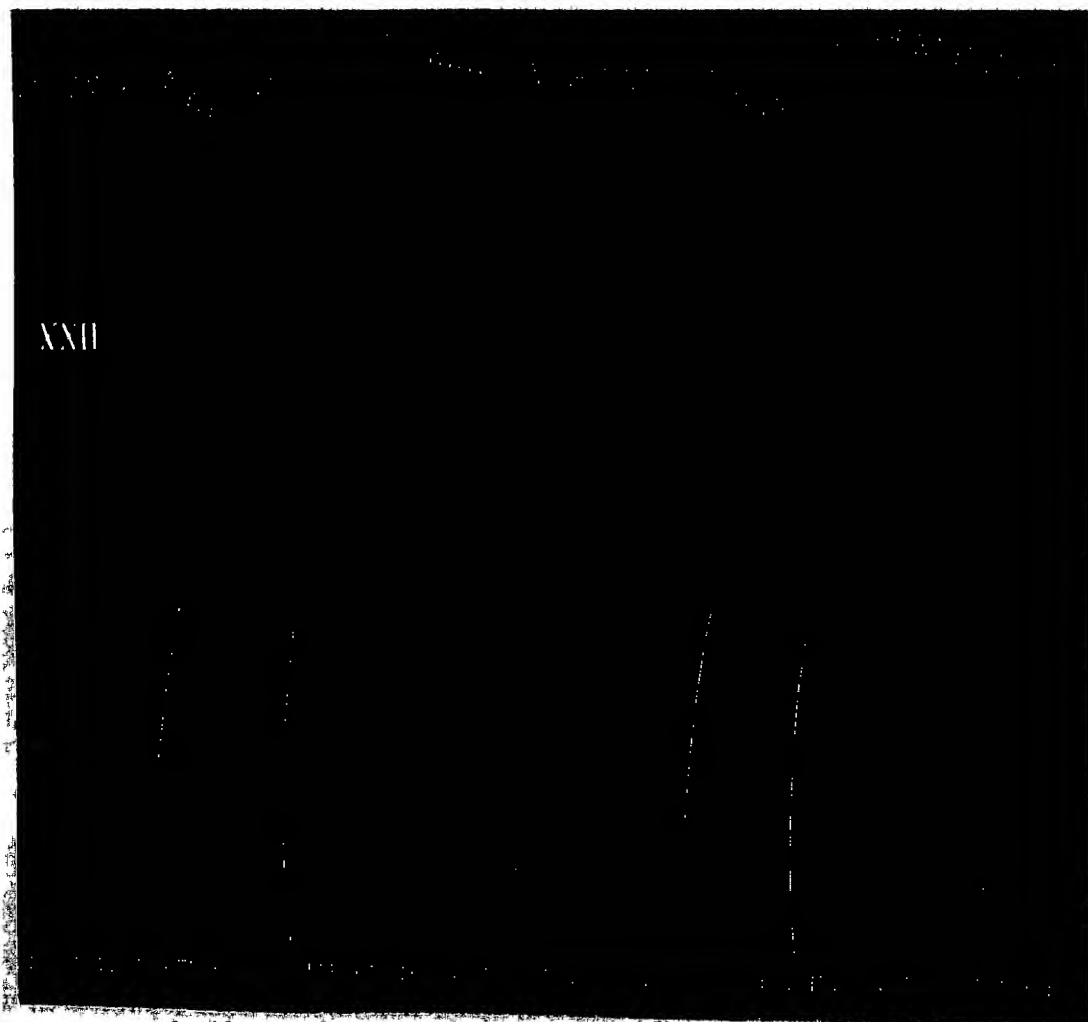
Lastly, we have already mentioned that in cases where long continued pressure has gradually caused paralysis of the vagal centres (loss of slowing), so that the heart commences to run at a rapid rate, subsequent section of the vagi has no effect on the already high blood pressure

A. (3). R The effect on respiration, the vagi being divided.

The effect on the respiratory movements of raising the intra-cranial pressure under these circumstances is almost always to produce an increase of movement, as follows —

(1) The vagal type of respiration may become enormously exaggerated, the pauses greatly drawn out and the movements forcible. (Tracing XXII.)

Tracing XXII.



The upper line is the tracing of the Blood-pressure, the middle that of the Respiration the lower that of the Time

(2) The division of the vagus when the pressure has already arrested respiration may furnish an inspiratory stimulus of complete adequacy, so that the respiratory movements recommence and continue (See Tracing XIX.) This is, no doubt due to the coincident rise of blood-pressure

(3.) Occasionally an inspiratory spasm may be evoked at the moment of putting on the pressure

Frequently acceleration of the rate of respiration was noted shortly before arrest occurred

*Division B — Examination of the Results obtained by directly raising the pressure in the fourth ventricle.*

As this forms a special division of the present research, we have postponed detailing the method of experiment until now

The occipito-atlantal membrane and part of the occipital bone having been removed, a small olive-shaped bag, measuring when collapsed only 0.5 cc, was inserted gently into the fourth ventricle by means of a probe, the direction taken being rather towards the raised up cerebellum, so as to avoid pressure on the floor of the ventricle. The bag was found to effect local distension of the ventricle, exactly according to the depth it was inserted.

By such direct pressure it was hoped that differentiation of the effects described in Division A might be obtained, and to a certain extent this succeeded.

The three "centres," analysis of which was desired, were of course:—

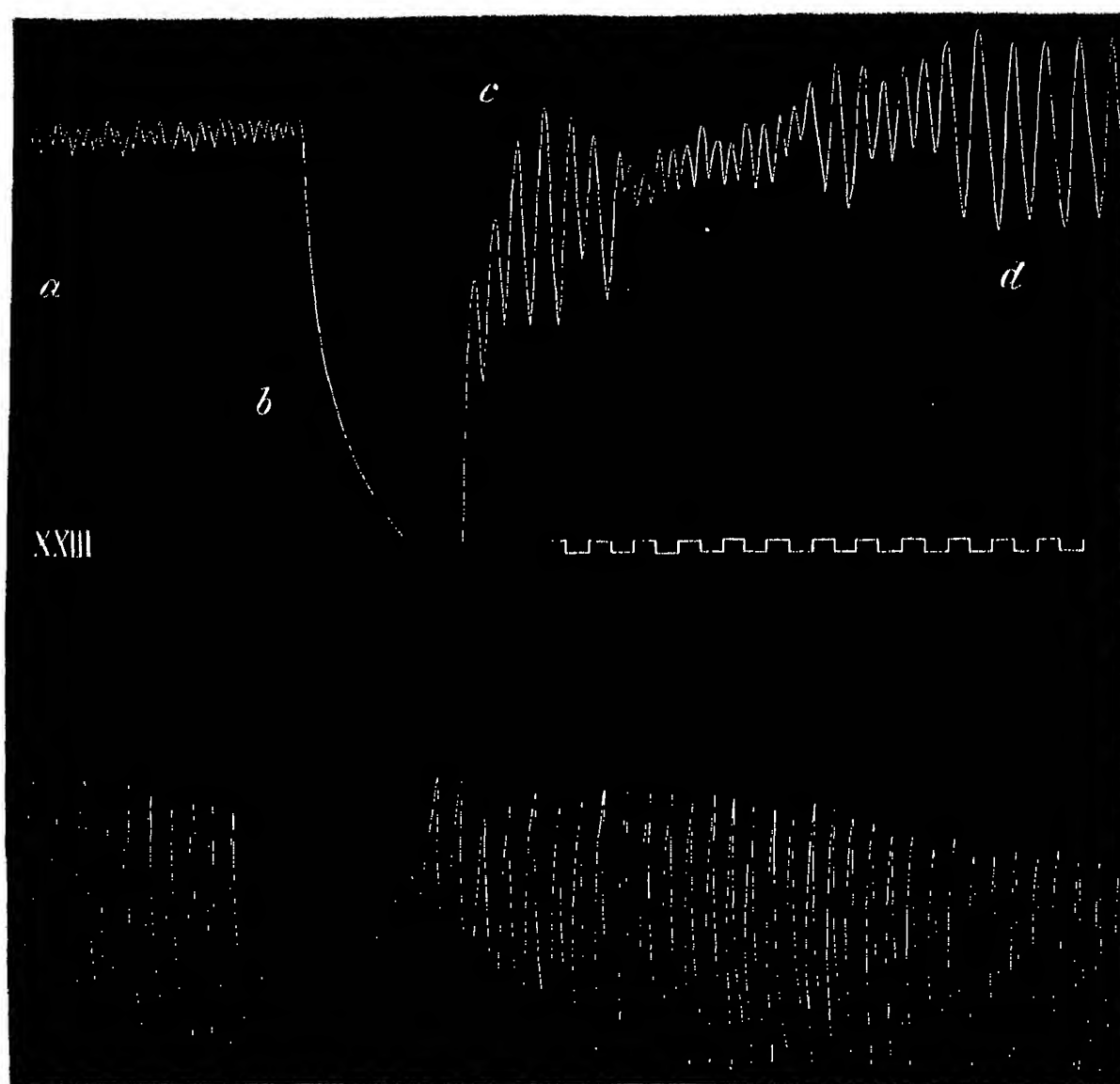
- (1.) The Respiratory
- (2.) The Vasomotor
- (3.) The Cardio-Inhibitory.

It goes without saying that the modes in which these centres were first excited and then paralysed resembled in every way those we have previously considered, so that the points we wish to emphasise now relate to the interaction of these centres more than the absolute changes in their functions. The results may consequently best be grouped in the following manner:—

- (a.) Affection of the respiratory centre without change in the cardio-inhibitory apparatus
- (b.) Affection of the cardio-inhibitory apparatus without alteration of respiration.
- (c.) Concomitant paralysis of the three centres.

(a.) The respiratory, we have seen before, is of all the bulbar mechanisms the most sensitive. While, however, as will be seen in Tracing XXIII, if the pressure be applied to the region of the calamus, both the heart's action and respiration are simultaneously arrested, the respiratory function can be gravely altered alone if the centre of pressure be shifted lower, so as to principally act upon the first segment of the spinal cord

## Tracing XXIII

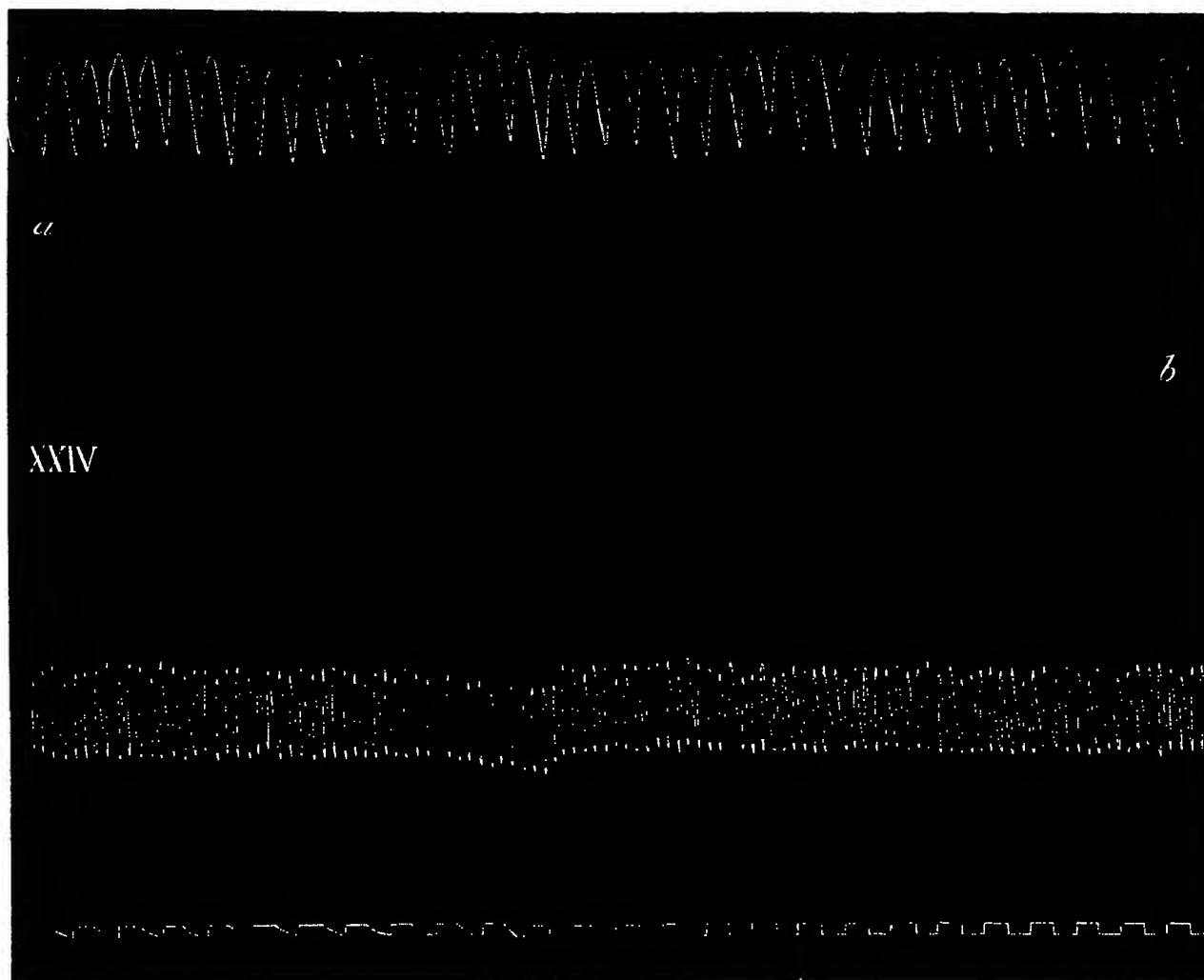


The upper line is the tracing of the Blood-pressure, the middle that of the Time, the lower that of the Respiration.

(b.) That the cardio-inhibitory apparatus can be excited without concomitant excitation (or paralysis) of the respiratory centre is shewn by Tracing XXIV., in which, after the pressure had been first applied to the upper part of the fourth ventricle, and then taken off, the heart's rate continued to be slow, and the systole prolonged, while the respiration went on at a rapid rate, almost three times that of the heart.

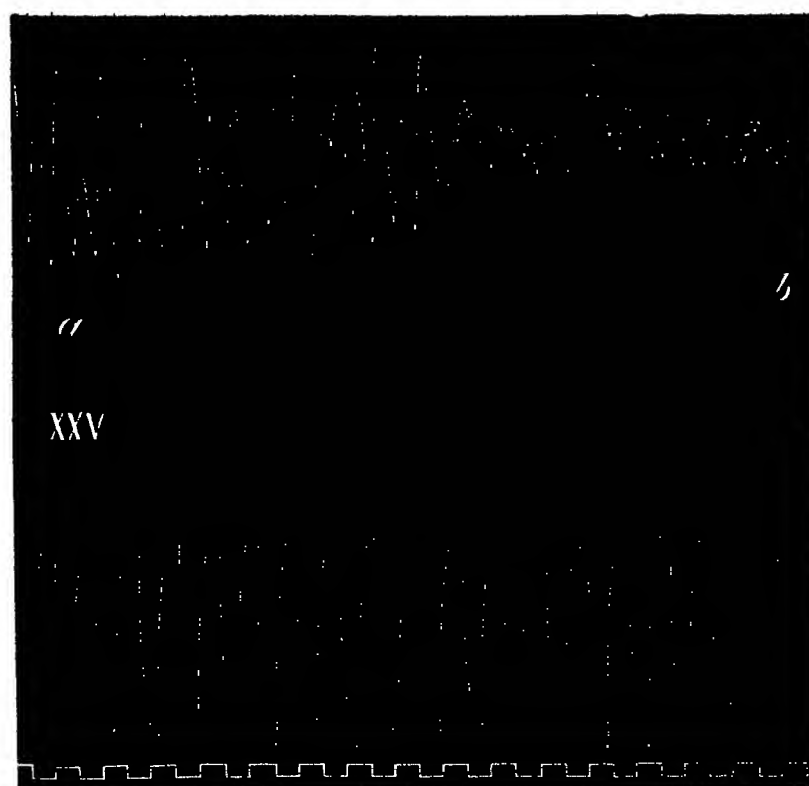
(c.) Paralysis of all three centres is well exemplified in Tracing XXV, where is seen the slow rate of the heart giving place to rapidity as the vagal centre loses its inhibitory influence, and, further, the respiratory centre having failed completely, artificial respiration is perforce employed. In the same tracing there is seen to be an absence of the usual pressor effect consequent upon paralysis of the vagal centre. Consequently, the vasomotor centre must be in part abrogated. That it was not wholly so was seen by the effect of asphyxia, but at least it was impaired. The centre of the pressure under these circumstances was in the middle of the ventricle.

## Tracing XXIV



The upper line is the tracing of the Blood-pressure, the middle that of the Respiration, the lower that of the Time.

## Tracing XXV



The upper line is the tracing of the Blood-pressure, the middle that of the Respiration, the lower that of the Time.



6 *Summary of Results*

We have, therefore, by means of an increase in intra-cranial pressure caused decrease and alteration of functional activity, partial or complete, of three "centres" existing in the medulla. The effect of the pressure has been both excitatory and paralytic, according to its degree, and the series of events followed one another in a definite order. We will summarise the facts observed under the headings we have already employed.

*The Heart*—Slight pressure reduced the rapid heart-beat of the Dog to 130 or so per minute in the same way as deep etherisation. Intermissions of the heart-beat sometimes occurred before any marked slowing. With further pressure the heart was slowed and arrested. The immediate removal of the pressure after arrest of the heart, or at most before the expiration of 10 or 20 seconds, allowed the heart to start again, but unlike the electrical stimulation of the vagus nerve, the arrest of the heart continued unless the pressure was removed. Artificial respiration cannot prevent the heart from being arrested, although a more severe pressure may be required to effect this than when artificial respiration is not in use. However, this power of arresting the heart is quickly weakened, and the heart starts again, whilst that pressure remains which just before arrested it, provided that the artificial respiration is continued.

After the removal of pressure, the slowing of the heart usually continued for some short time, and did not cease immediately; there being a gradual return to the normal.

When the pressure was continued, and artificial respiration at the same time kept up, the heart continued slow, and then gradually returned to its normal rate, as if the pressure had become compensated, and as if the cardio-inhibitory apparatus ceased to be stimulated. But with more severe pressure the change was different; the slow heart, after a period, quickened rapidly until it reached the rate which follows division of the vagi. This points to a complete paralysis of the cardio-inhibitory apparatus; but if the pressure were then taken off, and a pause made, it was found that the cardio-inhibition recovered, and that the heart could be slowed or even arrested again by pressure. But the paralysis of this cardio-inhibitory apparatus was more easily obtained on the second application of pressure.

*The Blood Pressure*.—The vasomotor "centre" was also at first stimulated, then partly stimulated, partly paralysed, and finally completely paralysed. With increased intra-cranial tension insufficient to slow the heart, the normal vasomotor curves were rendered more prominent, and the rhythmic character slowed, so that the curves appeared longer. With a rapid rise of intra-cranial tension there was only a slight rise (*i.e.*, excitation effect) of blood pressure in the Dog; but in the Monkey pressor influences at this stage were better marked. Depressor influence may be excited without any previous rise of blood pressure, and the blood pressure may fall greatly

before the heart is arrested, also it may persist after the heart has begun again, and only slowly disappear even when the vagi are divided. But this depressor influence is easily lost, so that on repeating the experiment a fall of blood pressure does not take place, nor can the heart be arrested, although it may be greatly slowed. When under this condition, the blood pressure may be about the normal level, but a further rise of intra-cranial tension may still further stimulate pressor influences, so that the blood pressure may rise to the level reached after division of the vagi, as shown by the absence of any further rise when this operation is performed. When the intra-cranial tension is relieved, the blood pressure returns to a level generally a little higher than normal, *i.e.*, when no depressor influences can be called forth.

With long-continued and severe pressure, and in spite of the continuation of artificial respiration, the pressor influences were lost, and the vasomotor tone was gradually reduced until the blood pressure fell to 30 mm Hg, *i.e.*, to about the level observed after division of the spinal cord below the medulla.

When both vagi are divided there is of course normally a rise of blood pressure. If depressor influences be active at the time the rise is only gradual, but when depressor influences have been lost, or are not active, the rise is as rapid as when there is no increased intra-cranial tension. The height reached when the vagi are divided whilst the intra-cranial tension is raised is much greater. But the actual amount of rise as before mentioned is dependent for its extreme development upon the pre-existent activity of pressor influences. The blood pressure may have been so raised in this manner that no further rise takes place on division of the vagi.

After division of the vagi the blood pressure can be raised higher still by the employment of artificial respiration, and by increase of the intra-cranial tension. Phenomenally high blood pressure we have thus produced, if at the stage just described attempts at natural respiration should occur during the artificial respirations. Nevertheless, the vasomotor tone is gradually paralysed (just the same as when the vagi are not divided) with a consequent fall of blood pressure, since at this low level 30 to 60 mm. Hg, there is no effect produced when severe intra-cranial pressure is applied, the only result in fact being to still further lower vasomotor tone. And this vasomotor tone, once lost, is not recovered from.

*The Respiration* — The uncertainty with regard to first principles concerning the action of the respiratory "centre" greatly hinders the distinction of the different stages of its disturbance by increase of the intra-cranial pressure. Still we believe that an excitatory and paralysing result respectively may be observed, although the various phenomena are not so clear as in the case of the heart. The excitatory effect appears to be evidenced by the inspiratory spasms we have often observed. The paralytic effect was shown to appear gradually by diminished extent of each movement, by slowing of the rhythm, and finally by arrest. Artificial respiration quickly removed the paralytic effect, and after cessation of the former a stage of apnoea occurred, followed by regular respirations. When more severe pressure was

used the apnoea did not appear, but after a relatively longer application of pressure respiration began immediately after the cessation of artificial aeration but with diminished extent. We did not obtain acceleration of respiration from increased intra-cranial pressure when etherisation was complete, except after division of the vagi.

We must now summarise the relations of the heart rate, the blood pressure and respiration to one another, when the intra-cranial pressure was increased.

If depressor influences were active and had not been impaired in any way, then the slowing of the respiration was accompanied by slowing of the heart and a fall of blood pressure. When the respiration was arrested the heart was greatly slowed, and then stopped. But if the depressor influence had been lost the heart was only slowed a little on the arrest of respiration, and there was no fall of blood pressure nor arrest of the heart, and the slight slowing was altogether lost when the heart was acting very quickly consequent upon paralysis of the cardio-inhibitory apparatus. The blood pressure affected the heart rate apart from any cardio-inhibitory effect, for after division of the vagi the heart became quickened as the blood pressure rose, and slowed as it fell.

Respiration was directly influenced by the blood pressure, as shown by the fact that a rise of blood pressure, the intra-cranial pressure remaining as before, tended to start respiration again. Respiration began again, moreover, after artificial respiration had been kept up a sufficiently long time for pressor influences to be established, although the intra-cranial pressure still remained at the height which had arrested the respiratory movements just before when the blood pressure was lower. And conversely, no regular respiration could be obtained with low blood pressure, owing to loss of the vasomotor tone. After division of the vagi under which circumstance a sudden increase of intra-cranial pressure caused a marked rise of blood pressure, we were able to excite respiration again by rapidly increasing the intra-cranial pressure, owing to its influence in further raising the blood pressure.

After division of the vagi, and after commencement of artificial respiration, if the intra-cranial pressure were increased beyond what had sufficed to stop the natural respirations until the blood pressure was raised from 320 to 360 mm. Hg, then natural respirations occurred amongst the artificial ones, and they reacted on the vasomotor centre producing the phenomenally high pressure before mentioned. We were able often to foretell that respiration was just about to begin by noticing a rise of blood pressure.

Artificial respiration had great influence in raising the blood pressure until vasomotor tone was abolished, then its efficacy was lost.

By means of our further experiments directly upon the fourth ventricle we have shown that respiration is arrested alone without slowing of the heart when the upper end of the spinal cord is pressed upon immediately below the calamus, although the blood pressure may naturally fall if the compression be severe. When respiration is

slowed or arrested along with slowing or arrest of the heart, and a fall of blood pressure is simultaneously produced, it is the lower portion of the floor of the fourth ventricle which is pressed upon

In the upper part of the fourth ventricle the heart may be slowed, and the blood pressure rise, without respiration being hindered in the least, or it may be even accelerated

Between these two points respiration is arrested and the heart slowed, while the blood pressure may fall slightly at first, but this fall is quickly changed into a rise above the normal

In a paper to follow this one, one of us will consider the results of electric excitation of the floor of the fourth ventricle, and we believe that we shall be able to show an exact agreement between the results obtained by the two methods of experiment, viz , pressure and excitation

TABULAR Description of Tracings (the small letters correspond to those on the tracings)

Tracing I EXPERIMENT D * 43 <i>Intermissions in the Heart Beats</i>	Rate of paper cm. per minute	Pressure in rubber bag mm Hg	Cranial content less in c c	Blood pressure mm Hg	Heart rate per minute	Rate of respiration per minute and Character of respiration
Pressure applied over the frontal lobe, between bone and dura mater						
Before the experiment	7			130 to 122	130	95 Normal
a Application of pressure	7	100		110 " 102	140	130 "
b. 40 seconds after a	7	100	1	122 " 116	140	130 "
NOTE.—The rise above the average level is due to the recoil of the mercury						
Tracing II EXPERIMENT D 71 <i>Abnormal Respiratory Variations in Blood Pressure</i>						
Pressure applied in the substance of the frontal lobe						
Before the experiment	145			150 " 142	175	90 "
a 2 minutes after the application of pressure	145	250	6	142 " 137	170	70 Deep inspirations at intervals
b 3	145	250	7	142 " 132	120	25 Pause longer, with inspirations of varying depth
c 4	145	250	7 2	142 " 135	110	9 Pause longer, with inspirations of varying depth
Tracing III EXPERIMENT D 60 <i>Vasomotor Curves Appearing and Growing Longer with Increasing Force.</i>						
Pressure applied over the cerebellum, between the bone and dura mater						
Before the experiment	145			130 " 114	110	80 Normal
a Application of more pressure	145	500	2 4	132 " 102	105	80 "
b. 30 seconds after a	145	500	3	140 " 110	90	75 ,
c Application of more pressure						
d 1 minute after c	145	550	3 2	130 " 110	110	80 "
e Application of more pressure	145	600	3 2	140 " 110	90	85 "

\* The letter D or M after the word experiment indicates the nature of the animal, i.e., whether Dog or Monkey is the number of the animal in the series employed

The number immediately following

TABULAR Description of Tracings—(continued)

	Rate of paper cm per minute	Pressure in rubber bag mm Hg	Cranial content less in c c	Blood pressure mm Hg	Heart rate per minute	Rate of respiration per minute and Character of respiration
<p>TRACING IV EXPERIMENT D. 96</p> <p><i>Slight Primary Rise of Blood Pressure</i></p> <p>Pressure applied anterior to frontal lobe between the dura mater and brain</p> <p>Before the experiment</p> <p><i>a</i> Application of pressure</p> <p><i>b</i> 30 seconds after <i>a</i></p>	14.5	.		160 to 148	130	90 Normal
	14.5	300		145 "	150	90 "
	14.5	300	6	160 "	150	85 "
<p>TRACING V. EXPERIMENT M. 43</p> <p><i>1st Part Primary Rise of Blood Pressure in the Monkey</i></p> <p>Pressure applied over the occipital lobe between the bone and dura mater</p> <p>Before the experiment</p> <p><i>a</i> Application of more pressure</p> <p><i>b</i> 10 seconds after <i>a</i></p> <p><i>c</i> 20 seconds after <i>a</i></p> <p><i>d</i> 24 seconds after <i>a</i></p> <p><i>e</i> Pressure removed</p> <p><i>f</i>. 10 seconds after <i>e</i></p> <p><i>g</i> 40 seconds after <i>e</i></p>	14.5	..	.	80 "	160	37 Normal
	14.5	500	5.1	85 "	160	35 "
	14.5	500	6	99 "	160	40 "
	14.5	500	6.8	140 "	140	Inspiratory spasm
	14.5	500	7	120 "	95	Arrested
	14.5		..	100 "	90	Arrested
	14.5		.	110 "	150	30
<p>TRACING VI EXPERIMENT M. 43</p> <p><i>Loss of the Primary Rise</i></p> <p>Pressure applied as in Tracing V</p> <p><i>h</i> Application of pressure</p> <p><i>i</i> 10 seconds after <i>h</i></p>	14.5	500	..	90 "	130	57 Normal
	14.5	500	5	66 "	70	20 Shallow, irregular

T. Descriptio of Tracings continued

	Rate of paper cm. per minute	Pressure in rubber bag mm Hg	Cranial content less in cc	Blood pressure mm Hg	Heart rate per minute	Rate of respiration per minute and Character of respiration
TRACING VII EXPERIMENT D 64						
<i>Depressor Effect Well Marked, Persisting after Division of Vagi</i>						
Pressure applied over cerebellum between dura mater and brain						
Before the experiment						
a. More pressure applied	145	500	32	150 to 142	150	60 Normal
b 10 seconds after a	145	500	35	148 , 136	130	50 "
c 20 seconds after a	145	500	4	128 , 120	120	60 "
d 30 seconds after a	145	500	4	104 , 92	120	70 Very shallow
e 40 to 45 seconds after a, division of both vagi	145	500	45	86	80	Arrested
f 1 minute after a, 15 seconds after division of vagi	145	500	54	82 , 70	120	"
g 1½ minute after a, 30 seconds after division of vagi	145	500	54	106 , 94	130	"
In 3 minutes after a, the blood pressure had risen to 190 mm Hg.						
TRACING VIII. EXPERIMENT D 96, Continuation of Tracing IV.						
<i>Slowing and Arrest of Heart and Respiration, the Recovery of the Heart Immediately on Starting Artificial Respiration</i>						
Pressure as in Tracing IV						
c. 1 minute after application of pressure	145	300	63	153 to 133	110	60 Shallow
d. 1½ minute "	145	300	64	139 , 87	70	Arrested
e. 1 minute 42 seconds after application of pressure	145	300	66	Zero	Arrested	"
f. 1 minute 54 seconds after application of pressure, artificial respiration started	145	300	68	Immediate rise	"	24 Artificial
g 2 minutes 20 seconds after application of pressure	145	300	7	143 to 125	115	24 "



TABULAR Description of Tracings—(continued).

Rate of paper cm per minute	Pressure in rubber bag mm Hg	Cranial content less in c c	Blood pressure mm Hg	Heart rate per minute	Rate of respiration per minute and Character of respiration
<p>TRACING IX EXPERIMENT D 96</p> <p><i>Arrest of the Slowed Heart after Removal of the Pressure, on Account of the Absence of Respiration</i></p> <p>Pressure applied anterior to the frontal lobe, between the bone and dura mater</p> <p>Before the experiment</p> <p>a 30 seconds after the application of more pressure</p> <p>b 44 seconds after the application, all pressure removed . . . . .</p> <p>c 4 seconds after b . . . . .</p> <p>d 12 seconds after c artificial respiration begun . . . . .</p> <p>e 30 seconds after d . . . . .</p>					
145					
145	400	5	160 to 144 142 „ 122	130 100	95 Normal 95 „
145			146 „ 100 Zero	70 Arrested	Arrested „
145			110 to 90	80	24 Artificial
<p>TRACING X EXPERIMENT D 81</p> <p><i>The Heart Re-starting after Arrest, but Continuing Slow</i></p> <p>Pressure applied in the fourth ventricle</p> <p>Before the experiment</p> <p>a Application of more pressure</p> <p>b 12 seconds after a</p> <p>c 12 seconds after b</p> <p>d 16 seconds after c, artificial respiration begun</p> <p>e 40 seconds after d . . . . .</p>					
145					
145	100	15	115 to 95 132 „ 76 Zero	90 50	30 Normal 50 Irregular
145	100	15	Zero	Arrested	50
145	100	15	„	„	Arrested
145	100	18	145 to 95	35	34 Artificial
<p>TRACING XI EXPERIMENT D 96.</p> <p><i>Arrest of Heart during Artificial Respiration, its Recovery, and the Appearance of Respiratory Variations in Blood Pressure</i></p> <p>Pressure applied anterior to the frontal lobe, between the dura mater and the brain</p> <p>Before the experiment</p> <p>a 40 seconds after application of more pressure</p> <p>b 42 „ „ „</p>					
145					
145	400	8	160 to 144 121 „ 41 Zero	130 65	95 Normal 24 Artificial
145	400	8		Arrested	24 „

TABULAR Description of Tracings—(continued).

	Rate of paper cm per minute	Pressure in rubber bag mm Hg	Cranial content less in c c	Blood pressure mm Hg	Heart rate per minute	Rate of respiration per minute and Character of respiration
<i>c</i> 1 minute after application of more pressure, pressure removed	14.5	..		Zero	Arrested	24 Artificial
<i>d</i> 40 seconds after <i>c</i>	14.5			130 to 58	" 50	24 " "
<i>e.</i> After a pause the heart started	14.5			162 " 102	80	
<i>f</i> After another pause, artificial respiration was stopped	14.5			170 " 122	90	18 Deep with long pauses
Natural respiration began						
<i>g</i> 1 minute after natural respiration had begun.	14.5					
TRACING XII EXPERIMENT 96						
<i>Arrest of the Heart, Starting again by Forcible Beats, Separated by Long Intervals</i>						
Pressure applied as in Tracing XI, after recovery						
<i>a.</i> 40 seconds after application of pressure again	14.5	300	7	152 " 134	100	55 Normal
<i>b</i> 1 minute after	14.5	300	7	Zero	Arrested	Arrested
<i>c.</i> 1 minute 22 seconds after application of pressure again	14.5	300	7	"	,	23 Artificial
After a pause, with artificial respiration continued, and re-starting of heart and rise of blood pressure						
<i>d</i> 3 minutes after application of pressure.	14.5	300	7.5	214 to 114	30	23 "
TRACING XIII. EXPERIMENT D. 95						
<i>Increased Rapidity of the Heart after Slowing as great as the Rate which follows Division of the Vagi.</i>						
Pressure applied anterior to the frontal lobe between the bone and dura mater						
Before the experiment	14.5	..		120 to 106	125	115 Normal
<i>a.</i> Application of more pressure	14.5	500	..	150 " 100	85	25 Artificial
<i>b.</i> About 1 minute after <i>a</i>	14.5	500	..	260 " 256	220	25. "
<i>c</i> Pressure removed						
<i>d</i> About 1 minute after <i>c</i>	14.5	.	.	115 , 65	80	40 Short inspirations

TABLE OF RESULTS OF EXPERIMENTS—(continued)

Rate of paper cm per minute	Pressure in rubber bag mm Hg	Cranial content less in cc	Blood pressure mm Hg	Heart rate per minute	Rate of respiration per minute and Character of respiration
TRACING XIV EXPERIMENT D 72					
<i>Rapidity of Heart Rate unmodified by Division of the Vagi</i>					
Pressure applied in the substance of the occipital lobe					
Before the experiment					
a Application of more pressure	400		130 to 125	150	85 Normal
b 1 minute after a, both vagi divided	400		244 " 240	210	36 Artificial
c 12 seconds after b	400		260 " 256	200	36 "
	400		260 " 256	190	36 "
TRACING XV. EXPERIMENT D 91					
<i>Fall of Blood Pressure preceding the Slowing of the Heart, and continuing after Recovery of the Rhythmic Heart Rate</i>					
Pressure applied anterior to the frontal lobe between the skull and dura mater					
Before the experiment					
a 30 seconds after the application of pressure	300	5.5	100 to 90	110	85 Normal
b. 1 minute after application of pressure	300	6	130 " 122 Zero	110	60 "
c 2 minutes after application of pressure, and 1 minute after b	300	6.5	75 to 55	Arrested	Arrested
				120	38 Artificial
TRACING XVI EXPERIMENT D 69					
<i>Depressor Influences absent, although the Pressure was applied for the first time, and also absent after the Arrest of Respiration</i>					
Pressure applied in the substance of the frontal lobe					
Before the experiment					
a Application of pressure	300		130 to 120	140	68 Normal
b. 34 seconds after a	325	4	52 " 40	95	90
c 20 seconds after b	350	5	68 " 50	85	70
d. 42 seconds after c	350	7	72 " 46	75	55
e Pressure removed	350		80 " 44	48	Arrested
f 10 seconds after e			68 " 32	35	Arrested
g Artificial respiration started					
h Natural respiration began					

TABULAR Description of Tracings—(continued).

	Rate of paper cm per minute	Pressure in rubber bag mm Hg	Cranial content less in c c	Blood pressure mm Hg	Heart rate per minute	Rate of respiration per minute and Character of inspiration
<p>TRACING XVII EXPERIMENT D 91.</p> <p><i>Depressor Effect absent when Pressure was applied for the Second Time</i></p> <p>Pressure anterior to frontal lobe between the dura mater and the brain</p> <p>Before second experiment .</p> <p>a 30 seconds after the application of pressure .</p> <p>b 1 minute 6 seconds after "</p> <p>c 18 seconds after b .</p>						
	14.5	300	5.8	134 to 126	105	55 Normal
	14.5	300	6.5	160 " 148	105	40 Pauses longer
	14.5	300	7	150 " 136	95	Arrested
	14.5	300		150 " 136	90	"
<p>TRACING XVIII EXPERIMENT D 43</p> <p><i>Pressor Influences causing a marked Rise in Blood Pressure, while the Heart was much Slowed.</i></p> <p>Pressure applied over the cerebellum between the dura mater and the brain</p> <p>Before the experiment .</p> <p>a Application of pressure .</p> <p>b. 15 seconds after a .</p> <p>c. 40 seconds after b .</p>						
	7	100	2	130 " 122	130	95 Normal
	7	200	4	100 " 96	170	
	7	200		110 " 64	40	
	7	200		205 " 150	40	
<p>TRACING XIX EXPERIMENT D 56</p> <p><i>Division of the Vagi releasing the Heart and Respiration from Arrest.</i></p> <p>Pressure applied over the frontal lobe between the dura mater and brain</p> <p>Before the experiment .</p> <p>a. 9 seconds after application of pressure</p> <p>b 24 " "</p> <p>c. 28 " "</p> <p>d 30 to 34 " "</p> <p>e 30 seconds after d .</p>						
	14.5	350	6	140 " 120	120	100 Normal
	14.5	350	7	128 " 108	130	140
	14.5	350	7	132 " 102	100	Arrested
	14.5	350	7	Zero	Arrested	Arrested
	14.5	350	7	Rise	190	Inspiratory spasm
	14.5	350	8	188 to 178		40 Deep

TRACING XX    EXPERIMENT D 60.					
<i>Further Rise of Blood Pressure on starting Artificial Respiration, the Vagi having been Divided, and sufficient Pressure to stop Natural Respiration employed</i>					
Pressure applied over the cerebellum, between the bone and dura mater.					
<i>a</i> , Artificial respiration begun					
<i>b</i> 20 seconds after <i>a</i>					
Rate of paper cm per minute	Pressure in rubber bag mm Hg	Cranial content less in cc	Blood pressure, mm Hg	Heart rate per minute	Rate of respiration per minute and Character of respiration
14.5	600	5	180 to 162	150	36 Artificial
14.5	600	5.2	280	?	36 "
TRACING XXI    EXPERIMENT D 62					
<i>Very High Blood Pressure after Division of Vagi</i>					
Pressure over occipital lobe, between bone and dura mater.					
<i>a</i> 2 minutes 20 seconds after application of pressure					
<i>b</i> 10 seconds after <i>a</i>					
<i>c</i> 20    "    " <i>b</i>					
<i>d</i> 10    "    " <i>c</i>					
14.5	400	6	400	?	33 Artificial, with natural respiration
14.5	400	6	378	?	33 Artificial, with natural respiration
14.5	400	6	400	?	33 Artificial, with natural respiration
14.5	400	6	326	?	33 Artificial only
TRACING XXII    EXPERIMENT D 74					
<i>Enormously Exaggerated Respirations of Vagal Type</i>					
Pressure applied in the substance of the temporal sphenoidal lobe					
Division of vagi and application of pressure					
14.5	.		135 to 130	140	2 Inspiration, length, 4.5 seconds







V *On the Organisation of the Fossil Plants of the Coal-Measures.*—Part XVIII

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Received January 22,—Read February 12, 1891

## [PLATES 25-28 ]

IN my last Memoir, Part XVII.,\* I called attention to a spore-bearing strobilus, first described by me, under the name of *Volkmannia Dawsoni*, in 1871, in the 'Memoirs of the Literary and Philosophical Society of Manchester' This latter description was based upon sections made from a small fragment for which I was indebted to my old auxiliary Mr JOHN BUTTERWORTH, of Shaw, near Oldham, in the autumn of 1870 Beyond two insignificant fragments, seventeen years elapsed before any additional example of this very rare strobilus was discovered Hence, during that interval, I had no means of confirming, or otherwise, the conclusions arrived at in that early Memoir Nevertheless, in my Part V of this series ('Phil. Trans,' 1874) having to deal with some allied forms of Asterophyllitean stems, I again referred to this plant I pointed out the resemblance between the forms of transverse sections of its central vascular axis (*loc cit*, Plate 5, figs 28, c, and 29) and those of the centres of the Asterophyllitean stems figured on Plates I., II., and III of the same Memoir The references to this fructification in Part XVII, mentioned above, were connected with my discovery of the vegetative stem of this plant, the structure of which further sustains my conclusions in my Memoir V., not that any *specific* identity exists, such as I fear some of my expressions in that Memoir might seem to imply, but that in any botanical classification, their positions, though they are generically distinct, must be very near to one another, especially so far as their vegetative organs are concerned More recently, as stated in a footnote to p 99 of Part XVII, Mr LOMAX, of Radcliffe, has brought to me a series of specimens which he has discovered and which are of considerable importance, since they make clear a number of features which have hitherto been obscure. On the other hand, several structures of importance, well shown in the specimens figured in my Memoir of 1871, are not preserved in my new examples. Hence, in order that all of what we know of this remarkable plant may be consolidated in the present

\* 'Phil Trans,' B, vol 181, 1890

examination of it, I have reproduced some figures of the more characteristic structures described in 1871.

As shewn in Memoir V, fig 28, transverse sections of the axial vascular bundle of this strobilus have a triangular form, the three projecting angles being broad and abruptly truncated. These features are illustrated by fig. 1, which represents this bundle as seen in the section in my cabinet numbered 1049. The mean diameter of this bundle, measuring from the truncated end of one angle to the more projecting angles of the other two, is about .05 of an inch. The breadth of each angle at its truncated extremity varies from .02 to .03. These measurements approximate closely to what I find in all my specimens, excepting one, of which I have two transverse sections (C. N. 1898, I and L), in which the maximum diameter of the bundle is about .0144, and that of the truncate extremity of the angle .0032, measurements the proportions of which approximate much more nearly to those of the young twig of *Asterophyllites*, fig 1, Memoir V, than is usual in the homologous bundle of *Bournanites*. The maximum diameter of the tracheids of this axial bundle, fig 1, is about .004. None of the other tissues which must once have filled the circular area  $\alpha''$  in the centre of which this bundle is placed, are preserved in any of my specimens, with the exception of the narrow line  $\alpha'$  of fig. 1, which shows no definite structure, neither have I been able to discover any indications of vascular threads passing outwards from the bundle to the surrounding tissues of the axis; yet it is scarcely to be doubted that some such extensions must have existed. Fig. 1, *b*, represents a small portion of the innermost surface of what remains of the axial cortex. This organ is seen more perfectly in fig 2, *b* (C. N. 1040 B), and a portion of the same is further enlarged in fig 3. Throughout the greater part of its thickness, this cortex chiefly consists of a rather open parenchyma (fig 3, *b*), but, at its outer border  $b''$ , the tissues are more dense and opaque. Longitudinal sections of this stem (fig. 4, *b*, C. N. 1050) show that these cortical cells are more or less elongated vertically; the outermost of them passing into the prosenchymatous condition shown in fig. 5.

Round the inner margin of this zone (fig. 2, *b*,) we find a number of small isolated clusters of tracheids. Three of these clusters are seen at *c* in the further enlarged figure 3. These tracheids must have been derived from the bundle, fig 1,  $\alpha$ , but as already stated, no traces of such an origin have yet been observed. Fig. 6 represents the most absolutely transverse section I have yet obtained of this strobilus, all the others in my cabinet being more or less oblique. This specimen was collected by Mr. LOMAX.

Figs. 4, 6, 7, and 8 demonstrate that at each node of the axis of the strobilus the cortex expands into a conspicuous disk. The diameter of this disk in the specimen fig. 7 has been about 156. At its free margin this disk subdivides into a verticil of numerous narrow ascending lobes, which for the present I propose to designate disk-rays. This disk chiefly consists of an aggregation of radially elongated parenchymatous cells (see fig. 5, *d*). A vertical section through it (fig. 4, *d*) shows that it is

thickest where it originates in a centrifugal extension of the cortical tissues, becoming gradually thinner as it ascends to its marginal fringe of disk-rays. In the obliquely transverse section, fig 2, one side of this disk has been intersected at  $d$ , and in fig 7,  $d$ , a wedge-shaped segment of a similar one extends outwards from the central axial cavity  $a''$ . The disk is crossed obliquely in the section of which fig 1 is the central axis, as shown at  $d$  in fig 9 (C N 1049 A). The section has passed through the saucer-shaped disk at a lower part of the node at  $d'$  where its tissues are blended with those of the cortex  $b, b$ , but the two structures separate at  $d'', d''$ , because, on the side opposite to  $d'$ , the section has crossed the disk and cortex at a level nearer to the centre of the internode above. We shall see directly that each of these nodal disks bears some important organs on its upper surface.

In figs. 4 and 8 we find the peripheral margin of each disk prolonged upwards and outwards at  $e$  into a circle of leaf-like extensions. These latter I propose, for the present, to designate disk-rays, for the purpose of avoiding any term indicative of the possible homology of these organs. Fig. 10 represents a tangential section of a strobilus made through three verticils of these rays,  $e', e', e'$ , in a plane a little outside the margins of the three corresponding disks. We here find that these disk-rays are arranged in symmetrical verticils, and are of fairly uniform shapes and dimensions. Their lateral diameter at this point is about 0.3, and their vertical thickness about 0.02. The same organs are seen at fig 2,  $e, e$ . Fig 11 is an enlarged transverse section of one of these rays from the section C N 1898 B. It has a very distinct quasi-epidermal layer of cells,  $\alpha$ , enclosing the area  $\alpha'$  which seems to be wholly occupied by parenchymatous cells, amongst which I can detect no traces of a tracheidal bundle. In fig 7 are remains of four or five of these rays, each having a diameter of about 0.2. Returning to fig 2 we find that at the two opposite points,  $e'$  and  $e'$ , the periphery of the strobilus is preserved in the section, which is not the case with the two intermediate spaces. At each of the regions  $e', e'$ , we have a mass of transverse sections of the more apical portions of the disk-rays, two of which are further enlarged in fig. 12. In each of these we still have the quasi-epidermal layer,  $\alpha$ , of fig 11, and at the centre of each ray,  $\alpha'$ , we have also the parenchyma already seen in the same figure, but at each of the two margins of each ray this parenchyma has disappeared in almost every one of the numerous examples which my cabinet contains of sections of the apical portions of these rays. I have obtained no clue to the cause of this disappearance. Here again, as in fig. 11, I can discover no traces of a vascular bundle in the internal parenchyma which remains. Each of these rays seems to consist wholly of cellular tissue.

The number of these disk-rays seen at the portions  $e', e'$ , of fig 2, makes it manifest that at each of these peripheral portions of the strobilus we have more of the disk-rays than could be supplied by one or even two nodal verticils. The thin extremities of the rays of each verticil must have been sufficiently prolonged to overlap, and assist to protect the three or four verticils of sporangia superior to the nodal disk of which each ray was an extension.

*Appendages to the thickened nodal disks*—Returning to the transverse section, fig 9, made through the most central part of a nodal disk,  $d$ , we find the circular line of small translucent points,  $f$ , the centre of each of which is occupied by a few barred tracheids. Fig 13 represents one of these points, further enlarged, in which  $f'$  represents the intersected tracheidal bundle, and  $f''$  some of the surrounding cells of which the disk is composed. It is obvious that these tracheidal bundles are not identical with those cortical ones seen at  $c$  of fig 3, because we find the representatives of these latter bundles at several points, as at fig. 9,  $c$ , along the inner border of the cortical zone  $b$ . But I expect that the two verticils are homologous ones. I believe that as these latter *cortical* bundles ascended to a higher node of the axis they would there bend outwards into, or at least send branches to, a disk circle similar to those at fig 9,  $f$ , now under consideration. Each of these latter points represents the base of a sporangiophore, of which very many spring from the entire upper surface of the nodal disk. The exact plan of distribution of these sporangiophores is not clearly made out. At fig 5 we have one,  $f$ , ascending from the *innermost* border of the disk,  $d$ , where the latter forms an axillary angle with internodal cortex,  $b$ . On the other hand in fig. 7, where the *outermost* border of the disk is subdividing into the disk-rays,  $e, e$ , it is still giving off similar sporangiophores at  $f$ . In fig. 8, in which the upper surface of the disk is intersected at least midway between the inner and outer border of that seen at  $d$  in fig. 6, we still find the bases of a number of sporangiophores springing from it. In fig. 2,  $d''$ , we see the same section of a disk as that represented at  $d$  in fig. 9; only in the former case, owing to the obliquity of the section, we can trace the outward and upward extension of the disk. Along its *upper* surface, represented in the section by its *inner* margin, we count at least thirteen of these sporangiophores, the bases of which are still united with the disk. One of these is further magnified in fig. 14, and shows its tracheidal bundle at  $f$ . In the section represented by fig. 28 of Memoir V., we have a section (C N. 1047) of a disk corresponding to fig. 2,  $d''$ , only crossing the organ at a line still nearer its peripheral margin, where it is even beginning to break up into its component disk-rays; yet even here we find a number of the sporangia organically connected with it. In fig. 10 we have a tangential section of a strobilus, cut vertically in a plane a little external to the margins of the disks, and consequently passing through three verticils of disk rays,  $e', e', e'$ , where they are free from their respective disks. Immediately above each of these verticils, we have at  $f, f$ , very distinct rows of sporangiophores, now wholly free from the disk-rays upon which they simply rest. All these combined facts demonstrate that we have in this strobilus a condition to which I have seen no parallel elsewhere.

There are many cases in which a single verticil of sporangiophores springs, like the solitary one,  $f$ , shown in fig 5, from each axil formed by the junction of the nodal disk with the internodal cortex. It is so in the strobili of *Calamites* described in my Memoir XIV., but in this case each sporangiophore carries all the four sporangia which occupy that radial segment of the internodal circle of which they form a part. The

sporangiophores of several species of *Palæostachya* described by WEISS arise from similar axillary positions. But in *Bowmanites* alone do we find a nodal disk occupying a comparatively enlarged area, from the entire surface of which numerous sporangiophores arise, each one of which, as will immediately be demonstrated, supplies a single sporangium. This is a peculiar condition which must not be overlooked when we endeavour to determine the homological relations of the various organs of fructification of the *Calamariæ*, including those of the recent *Equisetums*.

At the lower part of their course each of these sporangiophores of *Bowmanites* has a diameter of about 001. Good transverse sections of these, like that represented in fig 15, are numerous in my cabinet specimen numbered 1898 H, where an epidermal layer begins to be more clearly differentiated from the cells which it invests. In no case does a sporangiophore spring from a disk-ray. They are wholly confined to the disk itself. A further study of these organs must follow an examination of the sporangia of the strobilus. A glance at the various sections referred to in the foregoing pages will show that the interval between each pair of verticils of disks and disk-rays corresponds to an internode of the axis of the strobilus. Also, that each of these internodal areas is occupied by a single layer of conspicuous sporangia. Since these sporangia vary somewhat in size and shape they are not packed with exact symmetrical horizontality. The vertical sections, figs. 4 and 8, indicate that there were from two to three concentric circles of sporangia in each of these areas, and since the size of these sporangia varies but in a limited degree, it follows that the outermost circle has contained more than the middle one, as it in turn had more than the innermost. We see also, from fig 10, that the outermost ring, *g*, *g'*, extended beyond the periphery of the disk and was lodged between the two verticils of disk-rays, *e*, *e'*. In most of my sections these sporangia exhibit a rounded contour, but a broken fragment in my cabinet (C N 1055 A) shows that mutual compression has given to some of them an angular, pyramidal form, as is also seen at *g'* of fig 10. Their mean diameter approximates to about 06.

The sporangial wall consists of a single layer of simple cubical cells, with a thickness of about 003. These cell-walls exhibit no special structures such as are seen in the homologous ones of the living *Equisetums* and the Carboniferous *Calamostachys*, but we find some marked peculiarities where each sporangiophore is united to its sporangium. We have already seen, from fig. 10, that the sporangiophores, *f*, pass outwards from their origins on the disk to their several destinations in individual sporangia in a layer lodged between the upper surface of the former and the under surfaces of the latter. This seems to be true even of each individual sporangiophore and the sporangium to which it belongs.

From what is observable amongst the sporangia of the upper end of fig. 2, it appears that each sporangiophore becomes united to its sporangium not at its proximal but at its distal side. It first passes completely under the sporangium and then bends backward upon itself to join the peripheral side of that organ. This is distinctly

shown by the two sporangia  $f'$ ,  $f'$ . Ordinarily the entire interior of the sporangium is occupied by the spores, but in each of the two examples  $g$ ,  $g$ , of fig. 2, we find the peripheral end prolonged beyond the spores, and the small space thus produced is occupied by an extremely delicate form of parenchyma. From the two sporangia  $f'$ ,  $f'$ , we further learn that this parenchyma is but an extension into the sporangium of the delicate cellular tissue occupying the interior of the sporangium. The uppermost of the above two is further magnified in fig. 16. The first fact to be noted here is that the recurved sporangiophore,  $f$ , has enlarged as it approached the sporangium,  $g$ , from a diameter of '001, its size at its proximal end, to '0133. At the same time the cells of its outermost or epidermal layer have become much more conspicuously differentiated from the delicate parenchyma,  $f'$ , which they enclose. We further see that the wall of the sporangium is not only continuous with that of the sporangiophore, but that the one is merely an extension of the other. At  $f''$  the tracheidal bundle of the sporangiophore is in virtually the same condition as in the proximal part of the organ, but at  $f'''$ , as is so commonly the case amongst these vascular Cryptogams, where the sporangiophore joins its sporangium the tracheids have increased both in number and in size. We further see that where the delicate parenchyma,  $f'$ , comes in contact with the spores, it terminates in a sharply defined boundary-line, which may possibly be prolonged inwards so as to constitute a thin membrane lining the entire inner surface of the sporangium wall.

The spores, so densely packed in the interiors of the sporangia differ from all others hitherto obtained from Carboniferous fructifications. Their rather thin exosporium is thickened along coarse reticulated lines, from each of the junctions of which reticulations there projects an elongated radiating spine. The spherical body of the spore is usually about '004 to '0048 in diameter, whilst from tip to tip of the projecting spines it is about from '0048 to '0063.

Independent of the verticillate arrangement of its organs suggestive of a general relationship to the Calamarian family, this strobilus is very distinct from all the numerous known Calamarian fructifications. In its nodal disks with their disk-rays, it approximates to *Calamostachys* and to *Cingularia*, but it differs widely from both in the origins of its sporangia and their attachments to their sporangiophores. In the triangular section of its protoxyloid central axis, seen alike in the fruit and in the vegetative stem, it approaches very near to *Sphenophyllum* and to my *Asterophyllites*, the affinities of which were discussed in my last Memoir when recording the discovery of the stem.\* But here again all resemblances end. My specimens throw no direct light upon the foliage of this plant; but this deficiency is abundantly supplied by Mr BOWMAN's original specimen figured by Mr. BINNEY.† Externally its stem and leaves are exactly those of an *Asterophyllites*. The former was jointed, with very

\* Memoir XVII, p. 100.

† 'On the Structure of Fossil Plants found in Carboniferous Rocks.' Part II, Plate XII., figs. 1, 1a, 1b, 1c. Palæontographical Society's volume for 1870.



prominent nodes, and the latter were linear, unineined, and arranged in nodal verticils. The Calamarian affinities suggested by these facts are further supported by the Sphenophylloid structure of its vegetative axis described in my last Memoir. We thus obtain from *Bowmanites* a fresh illustration of the fact that the old genus *Asterophyllites* is a purely provisional one, comprehending several very different plants.

The plant has been obtained from the Calcareous nodules of Coals which have furnished us with so rich a harvest of new forms. I have received it from the Footmine near Oldham, from the hard-bed at Cinder Hills near Halifax, and from Dulesgate. For my specimens of it I have been indebted to Mr J. BUTTERWORTH, of Shaw, near Oldham, to Mr SPENCER, of Halifax, and to Mr LOMAX, of Radcliffe.

*Rachiopteris ramosa*

With the object of restricting, as far as possible, the multiplication of ill-defined genera, I have, in my preceding Memoirs, described a number of Fern-like objects under the provisional name of *Rachiopteris*. I have occasionally, for some time past, obtained portions of what appeared to be a distinct plant belonging to the above type, but which were not sufficient to satisfy me respecting the essential details of its organisation. Now, however, my cabinet contains a sufficient number of sections to make those details intelligible, a transverse section of the main axis of the plant is represented in fig 19.

The central vascular bundle, fig 19, *a*, consists of a dense aggregation of barred tracheids, the inner ones of which are rather smaller than those at its periphery. Most of the former have a diameter of 0008, whilst many of the latter reach 0016. The majority of the smaller ones are simply barred; but most others, especially those of larger size, are of the reticulated type so often met with amongst the Carboniferous plants, and of which two are enlarged in fig 25. This bundle was invested by a zone of small, thin-walled, parenchymatous cells, but which are not preserved in the section figured. It is seen in another section in my cabinet (C N 1918 A). The uniform composition of this latter zone gives it more the aspect of an inner cortex than of a concentric phloem. In this respect it corresponds with many similar ones in *Rachiopterides* that I have previously described, and of which the homologous relations are open to question. In the figure 19 this zone is only represented by the vacant space surrounding the central bundle *a*.

The thick and conspicuous outer cortex, *b, b*, consists of numerous strongly defined, vertically elongated, parenchymatous cells, intermingled with others, especially in its more external portions, of a more prosenchymatous type.

*The Branches*—These are given off in great numbers. It is not uncommon to see five or six primary ones, *d, d*, given off, even from a very thin transverse section like fig 19. Since these branches radiate equally in every direction, it is evident that figs. 19 and 20 were ascending aerial stems and not rhizomes. In fig. 20, which



represents a vertical section of the plant under consideration, these primary branches, *d*, are given off at a considerable angle, but more frequently, as in fig. 19, they appear to pass outwards through the cortex of the main axis more horizontally. This direction produces the abrupt change seen in transverse sections like fig. 19, *c'*, represented, still further enlarged, in fig. 28. The tracheids of the axial bundle, *a*, are intersected transversely, whilst those at *b*, going to the branch, are intersected more longitudinally.

Sections of the main stem, in whatever direction they are made, are always surrounded by a swarm of similar sections of the large and small branches, though of varying shapes and sizes. These are seen to some extent at *e*, *e*, in figs. 19 and 20; but they occur in far greater numbers in other sections in my cabinet (*e.g.*, C. N. 1018, 1018 A, and 1018 B). Fig. 20 is a longitudinal section of a specimen corresponding in all respects to fig. 19. In it we have the central tracheidal bundle at *a*, enclosed within its cortical cylinder, *b*, *b*. Large primary branches, each with more or less of its branch bundle, are seen at *d*, *d*. I have in the cabinet a tangential section (C. N. 1918 C) made from the same specimen as fig. 20, but passing through the external cortex. We learn from it that the secondary branches are given off irregularly and not in any defined order either of size or of position. Fig. 21 represents part of one of the larger of these branches. Other smaller ones are seen in figs. 22-23 and 24. Amongst the smaller ones like figs. 23 and 24, the bundle *a* is frequently pushed to one side of the cavity in which it is lodged, as if the remainder of the cavity had been occupied by a collateral phloem; but I am satisfied that fig. 22 represents the normal position of the bundle. In a few of these sections I see evidence that in these branches the bundle was surrounded by a cellular zone like that already described as investing the bundle of the central stem in the Cabinet specimen 1918 A. Sections still smaller than fig. 24 are common enough, in which the bundles consist only of one or two minute tracheids. Such sections as those smaller ones just described are wholly undistinguishable from those of other and different *Rachiopterides*. Indeed the variations in the size, form, and other features of these smaller branches afford a fresh illustration of their insufficiency as foundations whereon to establish distinct genera. Some of my sections, especially the Cabinet specimens 1918 C and 1918 D, afford clear evidence that the exterior of the cortex was more or less clothed with multi-cellular hairs. Fig. 27 represents two of these hairs from the former of the above sections, and fig. 26 is part of the cortex of the latter one with the hairs *in situ*. Both the sections belong to the same stem as fig. 20, in which also the bases of some of these hairs are seen at *g*, *g*. It is quite possible that this plant may prove to be merely a more fully developed and less hirsute form of the *Rachiopteris hirsuta* described in Memoir Part XV., in which case it may stand as *R. hirsuta*, var. *ramosa*. Beyond this its real affinities are, as yet, uncertain. Many of its features suggest a relationship with the Ferns, but since no traces of its foliage have yet been discovered, this affinity cannot at present be determined. It is a curious fact that we

have as yet only discovered the leaves of one of the many supposed Fernstems which I have described—and that is precisely the one (*Lygynodendron Oldhamium*) the general features of which, at the first glance, were the least suggestive of any affinities with the *Filicinae*. Most of our recent ferns have their vascular bundles composed of a xylem element associated with a concentric phloem, but this was certainly not the case with all the Carboniferous Ferns. In the *Myelopteris* described in my Memoir VII, I found vacant spaces associated with the vascular bundles, I erroneously confounded these spaces with the gum-canals which are so abundant in the same stems. Since that Memoir was published I have obtained fine specimens of the same plant, in which these vascular bundles are more perfectly preserved, and which show that the supposed canals in close union with the xylem of each bundle were really spaces from which a true phloem had disappeared. The specimens in question vary so much that it is difficult to say exactly what is the true relation of the phloem to the xylem in these plants, but the preponderant indication is that the bundle is a collateral rather than a concentric cone. In dealing with the primæval Ferns we must not expect to find in them the exact histological conditions that are characteristic of living ones. Hence for the present, notwithstanding its anomalous features, I am inclined to class *Rachiopteris ramosa* with the *Filicinae*. Some of my specimens of this plant were obtained by Mr BINNS from the Hard Bed at Halifax. For others from the same district I am indebted to Mr SPENCER, and my later ones have been collected by Mr LOMAX, of Radcliffe.

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### *Bowmanites Dawson*, WILLIAMSON

- Plate 25, fig 1 Transverse section through the axial vascular bundle of a strobilus *a*, the tracheids, *a''*, part of the area originally occupied by the innermost cortex, traces of which remain in the narrow bands *a'*, *a'*, *b*, a portion of the inner border of the outer cortex  $\times 50$  C. N, \* 1049.
- Plate 26, fig 2 Specimen in which an oblique transverse section has intersected three nodal and the same number of internodal verticils of organs *a''*, centre of the axis from which the bundle like fig 1 has disappeared, *b*, cortex of the internodal verticil, immediately below the disk *d*, *d*, a portion of the nodal disk, sustaining the uppermost of the three verticils of sporangia, *d''*, section through the nodal disk next inferior to *d*, and giving off sporangio-phores, *f*, from its upper border, *e*, *e*, transverse section of the disk-rays of the disk next below *d''*; *e'* *e'*, numerous sections of the elongated upper portions of the disk-rays of several inferior nodal disks, *e''*, basis of two of the disk-rays of the disk *d*; *f*, *f*, transverse sections of several sporangio-

\* As in previous memoirs, this symbol indicates the number at which the specimen referred to will be found in the author's cabinet

phores,  $f'$  and  $f''$ , instances of sporangiophores united to their several sporangia,  $g$ , sporangia of the uppermost of the three verticils;  $g'$ , the second and lower verticil of sporangia,  $g''$  the third and yet lower verticil of sporangia.  $\times 13$  C N., 1049 B

Plate 27, fig 3 A portion of the cortex,  $b$ , of fig. 2, further enlarged.  $b'$ , the inner parenchyma of the cortex,  $b''$ , its outer portion,  $c, c$ , cortical bundles of tracheids.  $\times 150$

Plate 25, fig 4. A vertical section through the centre of a strobilus  $\alpha$ , the vascular bundle corresponding to fig 1,  $b, b$ , the cortex,  $d, d$ , sections through the nodal disks,  $e$ , a disk-ray,  $f$ , a sporangiophore;  $g$ , sporangia.

Plate 26, fig 5 The axil,  $f$ , of fig 8, showing the base of a sporangiophore, and the cellular structure of the neighbouring organs,  $b$ , the cortex;  $d$ , the nodal disk,  $f$ , the sporangiophore.

Plate 28, fig. 6 Slightly oblique section through a node of a strobilus  $\alpha''$ , centre of the axis from which a vascular bundle, like fig. 1,  $\alpha$ , has disappeared. At the upper and left-hand sides of the figure the section has passed through a lower portion of the strobilus than elsewhere;  $d$ , the uppermost nodal disk;  $e, e$ , part of a verticil of disk-rays belonging to the disk next below  $d$ ;  $e'$ , sections of the upper portions of the disk-rays belonging to still lower disks;  $g, g$ , verticil of sporangia occupying the internodal area next below the nodal disk,  $d$ ;  $g'$ , part of a verticil of sporangia belonging to an internode below that occupied by  $g, g$ .  $\times 15$ . C N., 1051 C.

Plate 26, fig 7. Segment from the centre of a second oblique section, made from the specimen which furnished fig. 2  $\alpha''$ , central cavity of the axis;  $d$ , part of the nodal disk,  $e, e$ , portions of three of the disk-rays;  $f, f$ , three sporangiophores.  $\times 15$  C. N., 1049 C.

Plate 25, fig. 8 Tangential section from the same specimen as fig. 4, but made through the cortex outside the axial vascular bundle:  $\alpha''$ , central cavity of the axis,  $b$ , cortex of an internode;  $d$ , section through a nodal disk within its peripheral margin;  $d', d'$ , two opposite peripheries of a nodal disk;  $e, e'$ , disk-rays,  $f$ , bases of sporangiophores springing from the upper surface of the disk,  $d$ ,  $f, f', f''$ , sporangiophores springing from various parts of the surface of the disk,  $d'$ .  $\times 8$ . C. N., 1058.

Plate 27, fig 9. Part of a second obliquely transverse section of the same specimen as fig 2, made in a plane where the tissues of the disk  $d, d'$ , blend with those of the cortex  $b, b$ ;  $\alpha''$ , the central axial cavity,  $b'$ , the inner parenchyma of the cortex;  $c$ , small vascular bundles, like those,  $c$ , of fig. 3;  $f'$ , small circular areas underlying the bases of the innermost series of sporangiophores, each area containing a minute vascular bundle in its interior.  $\times 110$ . C. N., 1049 A.

Plate 25, fig. 10. Tangential section passing through three nodes and internodes of a strobilus, a little outside the margins of the nodal disks;  $e', e'$ , free disk-

rays intersected transversely;  $e''$ , longitudinal sections of two disk-rays prolonged beyond the outermost verticils of sporangia,  $f, f$ , transverse sections of sporangiophores proceeding to the more external sporangia;  $g$ , verticils of sporangia  $\times 8$  C N, 1045.

Plate 28, fig 11 Enlarged transverse section of a disk-ray near its base,  $a$ , epidermal layer,  $a'$ , internal parenchyma  $\times 250$  C N, 1898 B

Plate 27, fig 12 Transverse sections of two disk-rays made nearer to their extremities than fig 11,  $a$ , epidermal layer;  $a'$ , central portion of the internal parenchyma  $\times 40$ . C N, 1049 B

Plate 27, fig 13 One of the small circular areas,  $f$ , of fig 9, further enlarged,  $f'$ , central bundle of tracheids,  $f''$ , parenchymatous cells of the disk.  $\times 280$  C. N, 1049 A

Plate 26, fig 14. Transverse section of one of the small sporangia,  $f$ , projecting from the upper surface of the section through the disk,  $d''$ , of fig. 2,  $f$ , its tracheidal bundle  $\times 230$ . C N, 1049 B

Plate 28, fig 15 Transverse section of a sporangiophore further removed from its base than fig 14;  $f$ , its tracheidal bundle.  $\times 140$  C. N, 1898 C.

Plate 27, fig. 16 The uppermost of the two sporangiophores,  $f'$ ,  $f''$ , which are attached to their sporangia in the section fig 2,  $f$ , epidermal coat of the sporangiophore,  $f'$ , inner cellular tissue of the sporangiophore,  $f''$ ,  $f'''$ , tracheidal bundle of the sporangiophore,  $g$ , spores  $\times 40$  C N, 1049 B.

Plate 25, figs 17 and 18 Two spores  $\times 186$ . C. N, 1053.

*Rachiopteris ramosa*, WILLIAMSON.

Plate 28, fig 19 Transverse section of a stem,  $a$ , the central axial bundle composed wholly of tracheids,  $b$ , the outer cortex,  $c, c'$ , bundles of tracheids going off to primary branches,  $d$ , large primary branches.  $\times 30$  C N, 1851 A.

Plate 25, fig 20 Longitudinal section of a stem like fig 19,  $a$ , axial bundle of tracheids,  $b$ , cortex,  $d, d$ , primary branches,  $e$ , sections of secondary branches,  $g, g$ , cortical hairs  $\times 10$ . C.N, 1918 B

Plate 28, fig. 21. Transverse section of a primary branch,  $a$ , the tracheidal bundle,  $b$ , the cortical zone.  $\times 30$  C N, 1851

Plate 28, figs. 22 and 23 Transverse sections of secondary branches,  $a$ , tracheidal bundle,  $b$ , cortex  $\times 30$  C N, 1851

Plate 28, fig 24 Transverse section of a yet more distal twig  $\times 30$ . C N., 1851.

Plate 28, fig 25 Two of the reticulate tracheids of the axial bundle,  $a$ , of fig. 20.

Plate 26, fig 26. Portion of the cortex with some of its peculiar hairs *in situ*.  $\times 35$ . C N, 1918 D

Plate 26, fig. 27 Two isolated hairs like those of fig 26  $\times 35$ . C N, 1918 C.

Plate 27, fig 28. The base of the vascular bundle supplying one of the primary branches of fig 25, and illustrating the sudden deflexion of the branch tracheids,  $c$ , from those belonging to the central bundle  $a$ .



VI. CROONIAN LECTURE.—*On the Mammalian Nervous System, its Functions, and their Localisation determined by an Electrical Method.*

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[PLATES 29–35]

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CHAPTER I—INTRODUCTION, INCLUDING THE AUTHORS' METHOD AND THE PLAN OF THE RESEARCH.

IN the 'Proceedings of the Royal Society,' vol 45, 1889, p. 18 (Meeting of November 1, 1888), we published a preliminary account of some of the experiments of which the results are now given in full detail.

In that communication we stated that the object of our work then was to endeavour to ascertain the character of the excitatory processes occurring in nerve fibres, when, either directly (artificially) excited, or when in that state of functional activity, which is due to the passage of impulses along them from the central apparatus. The most important way in which such a method could be applied was obviously one which would involve the investigation of the excitatory changes occurring in the fibres of the spinal cord when the cortex cerebri is stimulated. We must at once assume that the motor side of the central nervous system is practically divisible into three elements — 1. Cortical centres 2. Efferent (pyramidal tract) fibres leading down through the internal capsule, corona radiata, and spinal cord. 3. Bulbo-spinal centres contained in the medulla and the spinal cord, and forming the well-known nuclei of the cranial and also of the spinal motor nerves

It had already been determined, both by direct observation and by the graphic method (1) that certain areas of the cortex were connected with definite movements of various parts of the body, and (2) that while the complete discharge of the cortical apparatus was followed by a very definite and characteristic series of contractions of the muscles in special relation with the particular point excited, the effectual removal of the cortical central mechanism and subsequent excitation of the white fibres passing down through the internal capsule, &c., led to the production of only a portion of the effect previously obtained from the uninjured brain

This method of observation in no wise showed what processes were actually occurring in the spinal and other nerve fibres, and although the ablation of the cortical centre, to a certain degree suggested the extent to which the cortex acted, nevertheless, it did not afford an exact demonstration of the same. Moreover, the data which the graphic method furnished were precluded, through their being muscular records, from determining what share, if any, the lower bulbo-spinal central nerve cells took, either in the production of the characteristic sequence of contractions or in the modification, whether in quality or in force of the descending nerve impulses during their transit.

It seemed to us that the only way to approach this subject would be to get, as it were, between the cortex and the bulbo-spinal system of centres. This would be accomplished if some means were devised of ascertaining the character of the excitatory processes occurring in the spinal fibres of the pyramidal tract, when upon excitation of the cortex, nervous impulses were discharged from the cortical cells and travelled down the cord.

The question as to the extent to which it is possible to obtain physical evidence of the actual presence in nerve fibres of excitatory processes and thus to arrive at reliable data for the comparison of their amounts is one which, up to the present, has been answered only indirectly, and that in two ways, firstly, by the extension of ~~HELMHOLTZ'S~~ classical experiment of determining the rate of transmission, and secondly, by observing those variations of electrical states in nerve fibres which



DU BOIS-REYMOND discovered to be invariable concomitants of excitatory processes. As will subsequently be shown in the historical retrospect, it is well known, through the researches of DU BOIS-REYMOND and others, that the fibres of the spinal cord, just as nerve fibres in the peripheral trunks, are characterised by showing when unexcited an electrical difference between their longitudinal surface and cross-sections, and furthermore, that when excited a well-marked diminution of this resting electrical state is produced in the fibres of the cord as in those of nerve trunks

Now since such excitatory variations in the electrical state are presumably parallel in time and amount with the presence in the nerve of the unknown processes termed excitatory, which a series of stimuli evokes, it was reasonable to presume, if the cortex were discharging a series of nerve-impulses at a certain rate down the pyramidal tract, that there would be a series of parallel changes in the electrical condition of the fibres in the cord tract, and that with a suitable apparatus for responding to such changes these might be both ascertained and recorded

If this could be done, then the character of the discharge of the cortical centre into the spinal cord would be, for the first time, definitely ascertained.

As has been said before, the graphic method to some extent suggested the solution of the problem, but the graphic method could not exclude, as this newer mode of investigation does, the bulbo-spinal centres. Judging from the rate of contractions of the muscles convulsed by excitation of the cortex, it was reasonable to expect that the variations in the electrical condition of the pyramidal tract might intermit fifteen or twenty times per second. If, therefore, they were to be observed or recorded, it was obvious that some instrument would have to be used capable of quickly responding to very minute electrical differences succeeding one another at very short intervals of time. The only instrument available for this task is LIPPMANN's electrometer, and, as we have stated in our previous communication, we had the advantage of the assistance of Mr G F BURCH in obtaining several very sensitive instruments.

This instrument in addition presents the invaluable advantage of its movements being easily recorded by photography, as originally described by BURDON SANDERSON and PAGE. Such records are given in our previous paper in the 'Proceedings'; they were from the first so definite, and so constant, that they enabled us at once to pass on to a further development of the same method. It occurred to us that the method afforded a means, not only of discovering the rhythm of the nerve disturbances as they pass along the spinal channels, but also of investigating the line of communication existing between separated nerve centres, the mode of discharge of such centres, and the determination of the direct paths, whether afferent or efferent in the structure of the central nervous system. It is this last wider application of the method to which we wish particularly to draw attention in the following pages, inasmuch as although it has hitherto been possible by means of division or ablation of certain portions of the central nervous system, *e g*, the spinal cord, to trace by

the loss of function the probable paths of transmission of afferent or efferent impulses, yet such a mode of experimentation is always open to very grave disadvantages and sources of fallacy. Such, for example, is the always recurring possibility of functional changes proceeding beyond the desired lesion, &c

The accomplishment of this further purpose, viz, the localisation of both paths and centres by ascertaining the excitatory electrical effects in relation with them, was one of the main objects we had in view.

In carrying it out we found it was unnecessary to employ the electrometer, and, in fact, that it was advantageous to use the galvanometer, the record of which could be more easily and more accurately noted, since its graduation admits of far higher magnification. Moreover, with this instrument it was possible, by employing a series of stimuli, of known number and duration, to obtain quantitative results of definite comparative value, as will be shown further on; and thus to compare the electrical effects evoked (1) in different central paths by direct stimulation of these, and (2) in any one path by excitation of different regions.

The plan upon which the present paper is framed is, first, to give a historical retrospect of the work of authors who have opened up the study of electrical changes in the central and peripheral nervous system, second, to describe at length our mode of experimentation, with special reference to the modifications which we have introduced, then to compare roughly the results we have obtained by our present method with those which had been previously ascertained by the graphic method, and so introduce the description of the facts which we have discovered, elucidating the physiology of the spinal cord both in its relation to the higher centres and to the peripheral nerves. In describing the detailed results of our experiments we have found that it is difficult, from the extent of ground covered by the subject, to adopt a convenient arrangement of facts, and mode of describing the same, which are free from the fault of repetition. We finally determined to gather the results together into definite groups, each associated with the excitation and investigation of particular regions, and refer in the briefest manner to any important principles which were not directly elucidated by, but only involved in, the particular experiments under consideration. Finally, we give at length a summary of the general conclusions which we consider we are justified in drawing from our experimental results.\*

\* We here wish to express our great indebtedness to Professor BURDON SANDERSON for placing at our disposal the instruments and equipment of the Physiological Laboratory of the University of Oxford. We are also under especial obligations to Mr G. F. BURCH, whose constructive skill provided us with the requisite electrometers, and who very kindly gave his assistance in preparing our photographic records.

Finally Dr. HOWARD TOOTH has very obligingly carried out the laborious task of the microscopical investigation of the spinal cords in those cases where we performed the section of columns antecedently to the special experiments of the present research.

The expenses of the present investigation have been defrayed by grants from the Scientific Grants Committee of the Royal Society, and from the Scientific Grants Committee of the British Medical Association.

## CHAPTER II—HISTORICAL

We consider it advisable to give a brief sketch or rather catalogue of the chief facts which have been ascertained concerning the specific function of nerve centres, and the conductivity of nerve fibres, so far as the central nervous system is concerned, in order that the various points we raise in the rest of the paper may be rendered more intelligible when the results obtained by our method are contrasted with those discovered by other means. It is naturally impossible for us to give on the present occasion a complete history of this vast subject, we would only, therefore, allude to those points towards the further elucidation of which we have directed the present research. The procedures employed by various authors with the exception of the galvanometric method may be enumerated as follows —

1. Electrical and other stimulation with direct observation of the phenomena evoked
2. Stimulation with graphic record of muscular and other movements produced
3. The method of anatomically observing the degeneration of nerve fibres consequent upon their separation from nerve centres with which they are in functional relation.
4. The embryological method of observing the development or differentiation of tracts and fibres

Of the foregoing methods, the first was the one by means of which the principles of localisation were earliest determined, and in this connection it is scarcely necessary to do more than allude by name to HITZIG and FRITSCH, FERRIER, MUNK, LUCIANI, ALBERTONI, and others. The results they obtained are to be classed with those gained by means of the second method of recording muscular and other movements, employed in the analysis of the functions of the central nervous system for the first time by FRANÇOIS FRANCK and PITRES, and in the subsequent investigations of BUBNOFF and HEIDENHAIN. They are open to the same objection, viz, that since they involve motor function they necessarily exhibit the activity of two sets of central mechanisms, and that therefore they only indicate the functions of the paths which run in the central nervous system in so far as these functions are modified by those paths being intimately connected with the lower or bulbo-spinal centres.

The degeneration method, in which localisation of a nerve path is accomplished by means of studying the retrograde changes which nerve fibres undergo when they are cut off from the lowest nerve centre, with which they are in relation, should they happen to be paths for ascending transmission, or *vice versa* from the highest nerve centre for descending transmission was initiated by TURCK and followed up more especially by CHARCOT and his pupils, as well as by a large number of investigators, and neuro-pathologists of all countries. This method is not free from possible error, since in the case of nerve channels connected at each end with central structures, we do not yet know what the nature of the connection must be which enables the nerve channel to successfully resist degeneration. Therefore, while the

existence of degeneration furnishes us with positive evidence as to the presence of a direct path, its absence does not exclude the existence of such a path.

The embryological method, which affords a very fair control of the degeneration method, was instituted by FLECHSIG and has since been extended by BECHTEREW and others. It gives a fair indication of the proportionate number or quantitative relation of the elements which go to make up any one channel, whether direct or indirect, but beyond this, and the all important localisation of position, it does not carry us. By a special histological method, introduced by GOLGI, the anatomical relation of the paths in the developing cord have recently received a fuller demonstration, at his hands as well as KOLLIKER'S, RAMÓN Y CAJAL'S and others.

It will be convenient to tabulate the facts according as they relate to

### I. Centres.

### II. Paths

### I CENTRES.

#### *Functional Activity of Centres.*

As regards Centres, the position assumed in the introduction\* is, we believe, as a matter of fact, tacitly in the minds of observers, if not admitted, and the influence of "basal centres" is not so overwhelmingly important as originally supposed by the older observers. To conveniently combine, therefore, the results without doing violence to the theoretical views expressed by anyone, it is only necessary to arrange the facts in relation to the part which is the seat of experimental investigation

#### A. Cortex.

(1.) *Latent Period*.—The loss of time which intervenes between the application of the stimulus to the cortex and the commencement of the resulting muscular contraction is .06 on the average in the Carnivora. (FRANCK and PITRES, BUBNOFF and HEIDENHAIN, SCHÄFER, ourselves)

(2.) *Excitability*.—This property of the cortex is greatly altered, *i.e.*, either increased, or diminished by—

(a) Severe hæmorrhage ; (b) deep anæsthesia, (c) cooling, (d) drying, (e) fatigue, (f) peripheral stimulation of the functionally corresponding and other parts of the body. (BUBNOFF and HEIDENHAIN, BUZZARD, EXNER.)

The latent period may vary from the effect of any of these causes as well as from the intensity of the stimulus. (BUBNOFF and HEIDENHAIN and other authors.)

\* *Viz.*, that the plan of the central nervous system, as regards its "motor" side, consists in a cortical mass of grey matter, and a corresponding mass in the bulbo-spinal part of the central neural axis, with segmental representation of function, while that finally these two great central apparatuses are connected by the direct paths known as the pyramidal tract or excitable fibres of the corona radiata internal capsule, and, we must add, of the lateral column of the spinal cord. According to this view the basal centres and cerebellum act on the direct motor apparatus, if at all, as reinforcing mechanisms

(3) *Mode of Discharge*.—The impulses generated in the cortex, and which pass down to the muscles may, according to the duration and intensity of the stimulus, be of the nature of (a) single discharges producing one muscular contraction; or (b) compound discharges producing tonic muscular contraction, or (c) a combination of tonic and clonic contractions. (FRITSCH, HITZIG, FERRIER, MUNK, FRANCK, and all other authors) This last combination is to be looked upon as the complete discharge of the cortex, *vide infra* and pp. 345–349, &c

(4) *Nature of the Discharge*—(a.) The single muscular contraction is more prolonged, and ceases more gradually than that elicited by a single stimulus applied to the motor nerve. (FRANCK, confirmed by ourselves)

(b) The tonic contraction is regarded by most authors as a fusion of contractions evoked by many discharges. (FRANCK, SCHAFER and HORSLEY, *vide infra* “*Corona Radiata*”)

(c) The tonic and clonic contractions occur in the order mentioned, and are to be regarded as the muscular response to a complete cortical discharge, *i.e.*, comprising a primary effect and after-effect

(d) The rate or rhythm with which these muscular responses\* appear to succeed one another has been variously estimated by different observers in different animals and with different instruments, and has been ascertained to be from 8 to 10 per second.

(5.) *Relation of the Discharge to the Parts of the Body*.—(a.) Localisation of the representation of the gross divisions of the body to definite areas of cortex (FRITSCH and HITZIG, FERRIER, MUNK, LUCIANI, SCHAFER, BEEVOR, HORSLEY)

(b) Localisation of the representation of segments of the gross divisions to definite areas of cortex. (BEEVOR and HORSLEY.)

(c.) Localisation of the representation of the character of the various movements of segments to definite areas of cortex (BEEVOR and HORSLEY.)

## B. *Spinal Cord*

Under this heading we will group the phenomena associated with the functional activity of the system of bulbo-spinal centres, *i.e.*, those in which the efferent paths terminate. It may not be superfluous to add that the information furnished by the graphic method does not differentiate the complex structure of a bulbo-spinal centre, and that it can only yield a record of the combined action of mainly afferent and mainly efferent corpuscles in the posterior and anterior divisions of the grey matter. All methods of observation hitherto employed involve the activity of the whole apparatus, and this must be borne in mind in considering the following facts

\* The tracing waves indicating the contractions are frequently summated (HORSLEY)

Quite recently the value of these waves as indications of rhythmical nerve discharges has been contested (WEDENSKII, HAYCRAFT)

(1) *Latent Period*—The interval of time occupied in the passage of a nerve impulse from the afferent to the efferent side of a (reflex) bulbo-spinal centre is given on p 481, to which reference is directed (WUNDT, EXNER, and others)

(2) *Excitability*—This function of the grey bulbo-spinal matter is modified by the same causes as those which influence the Cortex, see pp 272 and 483

When the excitability of the cord is raised, *e g*, that of the distal segments after section, these latter may discharge in a coordinated fashion, see p. 423, as was first observed by SCHIFF

(3) *Mode of Discharge*—The bulbo-spinal centres, like the cortex, present three modes of discharge, but not in the same degree, *e g.*, the combined sequence of tonus and clonus though sometimes present, see pp. 483–499, nevertheless occurs but rarely. Further, as evidenced by muscular responses, the bulbo-spinal centres appear to discharge at regular intervals under certain conditions of isolation and excitation, *e g*, ankle clonus (V H). For further detail see p 483.

(4) *Nature of the Discharge* (a) As in the case of the cortex cerebri the character of the muscular response to excitation of the cord is different from that seen when the excitation is directly applied to the nerve

(b.) The tonic contraction is usually developed more rapidly than that obtained from the corona radiata.

(c) The rhythm of the intermittent muscular contractions, fused or not, is from 8 to 10 per second or frequently the early multiples of this rate

(5) *Relation of the Discharge to the Parts of the Body*.—(a.) Localisation of the representation of the gross divisions of the body to different regions of the bulbo-spinal apparatus is well marked (All authors)

(b) Localisation of the representation of the segments of the gross divisions and the character of their respective movements to different root-origins in the grey matter (FERRIER and YEO, SCHIFF, FORGUE, BEEVOR)

## II PATHS

### *Functional Activity of the Efferent Paths*

The graphic method only permits of a limited analysis of paths, *i e*, fibres, inasmuch as there is of necessity included the bulbo-spinal system of centres for the purpose of giving the muscular contractions used for record. Hence no result by the graphic method can be regarded as pure; moreover, it only furnishes information upon the functions of efferent paths

In fact, there is no direct evidence forthcoming from any method of observation, except that of the galvanometer, to prove that the paths themselves in the cord are excitable. Indeed, it has long been held by many physiologists that all effects obtained from stimulation of the spinal cord are due to primary and progressive



excitation of reflex centres (SCHIFF, CHAUVEAU). Consequently, it must be understood that the following enumeration of facts is written and arranged in the light of our experimental results, set forth in the present paper

### A *Corona Radiata.*

(1) *Latent Period*—The loss of time intervening between the moment of application of the stimulus to the corona radiata and the commencement of the resulting muscular contraction is usually 0.4 sec (FRANCK and others)

(2) *Excitability*—The excitability of the fibres rapidly falls upon their exposure VULPIAN showed that relatively the excitability of the corona radiata was higher than that of the cortex. In this he was confirmed by the observations of BOCHE-FONTAINE, COUTY, ASCH and NEISSER, and others.

(3) *Mode of Discharge*—The muscular contraction may be (a) a single twitch, or (b) a tonus. The combination we have termed the complete cortical discharge, and consisting of tonus and clonus, is never seen where the cortex is absolutely removed (FRANCK, BUBNOFF and HEIDENHAIN in part, HORSLEY, SCHAFER and HORSLEY)

(4) *Nature of the Discharge*—(a) The tonus observed is regarded as a fusion of muscular responses which commence and end sharply with the beginning and end of the excitation

(b) The rate of recurrence of the individual responses is unknown.

(5) *Relation of the Discharge to the Parts of the Body*.—Localisation of gross divisions of the body to certain fields of fibres issuing from cortical centres (all authors named above)

### B *Internal Capsule*

(1) *Excitability*—The excitability of the fibres forming the internal capsule is very high (FRANCK, GLIKY, BEEVOR and HORSLEY.)

(2) *Mode of Discharge*.—Indistinguishable from that of the corona radiata, *quod vide*

(3) *Nature of Discharge*—Ditto

(4.) *Relation of the Discharge to the Parts of the Body*—(a) Localisation of the representation of the gross divisions of the body to limited fields of fibres (FRANCK and PITRES, GLIKY, BEEVOR and HORSLEY)

(b) Localisation of the representation of segments of the gross divisions of the body to definite fields of fibres. (BEEVOR and HORSLEY)

(c.) Localisation of the representation of the character of various movements of segments to definite fields or bundles of fibres. (BEEVOR and HORSLEY.)

### C. *Crus Cerebri*

(1) *Excitability*.—The excitability of the fibres has been determined by many observers. (BUDGE and others)



(2) *Relation of the Discharge to Parts of the Body* —Localisation of the representation of the gross divisions of the body to certain fields of fibres (BRISSAUD and others)

## D *Spinal Cord*

It will be scarcely realised, except by those who have made a special study of the literature of the physiology of the spinal cord, how little has been done which would enable us to carry out, strictly speaking, the differentiation of the subject of conduction in that organ, by arranging the facts in the same way as we have just done for the higher parts of the nervous system. So much so is this the case that we do not intend to do more at this stage than indicate what we believe to be a fair estimate of the experimental work already accomplished. In introducing our own work later on, which directly bears on the points at issue, we shall draw attention to many of the more salient details which require attentive discussion. We will, therefore now content ourselves with furnishing a general review of the function of conduction in the cord. We may note in passing that almost all the literature is to be found in the writings of VON BEZOLD, ECKHARD, GRUNHAGEN, SCHIFF, IMMANUEL MUNK, and others. We would, in the first place, urge, what we have reason to do with greater weight later, that not one of the foregoing methods, *i.e.*, graphic degeneration, embryological, &c, is capable of answering the question of conduction or its localisation in an absolute manner. The great difficulty in considering conduction by the cord is the disseverance of the action of the bulbo-spinal centres from that of the nerve fibres which happen to pass through or by them, and this difficulty does not appear to us to have met with the amount of attention that it would naturally seem to deserve. In fact, to our mind the galvanometric method is the only means within our reach at present by which a solution can be arrived at, and even that method requires to be considerably further elaborated.

Dividing conduction in the spinal cord into the two great classes of—

- 1 Conduction of impulses downwards,
2. Conduction of impulses upwards;

we are able to summarise the facts which appear to be thoroughly reliable as follows —

(1.) *Conduction of Impulses downwards* —In Man and the highest Apes direct conduction downwards, *i.e.*, from the cortical centres to the bulbo-spinal system, appears to be provided for in the upper half of the spinal cord by both the anterior column, close to the margin of the anterior fissure, and, speaking roughly, by a triangular area in the posterior part of the lateral column, just external to the posterior horn of grey matter.

(2.) *Conduction of Impulses upwards* —There is known to be an entrance from each posterior root into the postero-external column of fibres, which run directly from the ganglion of the posterior root as high as the medulla oblongata. These direct fibres

are further known to gradually tend towards the middle line of the cord as they are displaced by others entering the cord in proceeding upwards. Further these direct fibres are strictly unilateral, so far as is known at the present time.

There are, in addition, also other known systems of ascending channels, but these are not directly continuous with the root, but start indirectly from central mechanisms which, to judge from the degeneration method, although this is of course not absolute, appear to intervene. These are (1) the direct cerebellar tract which runs up the posterior and outer surface of the lateral column, and (2) the antero-lateral tract which occupies a similarly lateral position further forwards on the margin of the cord.

In addition to the foregoing, there is some evidence to show that internuncial fibres run in the lateral column in about the inner third of its centre, or a little posteriorly to this point. Of the existence of channels for transmission of impulses upwards in the opposite posterior column to the side of the root by which they enter the cord nothing is known for certain.

### *History of the Galvanometric Method of Determining the Action of the Nerve Centres and the Course of Nerve Channels*

As we have before frequently acknowledged, the real basis of the galvanometric method was the discovery by DU BOIS-REYMOND\* of the negative variation produced by excitation in the resting electrical difference of a nerve path. Since that discovery, the idea has doubtless occurred to various physiologists that, by this means, we might discover the mode of functional activity of nerve centres. CATON† was the first to our knowledge who directly employed the galvanometric method of determining such variations for the investigation of the activity of nerve centres, and the localisation of the same. He connected points on the external surface of the cortex with the galvanometer, and he found that the uninjured external surface of the brain was usually positive to a section of the same. When any part of the cortex thus investigated was thrown into activity, the resting difference showed distinct negative variations. Thus, in the Monkey, after the cortex had been prepared and the electrodes applied to the centres (FERRIER) of rotation of the head and mastication, the negative variation or action current showed itself when these movements were performed. Further, in the Rabbit, when the area of the cortex which subserves the movements of the eyelids was investigated, the negative variations showed themselves when the opposite retina was illuminated. SETSCHENOW‡ was the first to our knowledge who connected the medulla oblongata with the galvanometer. He noticed certain periodic variations in the resting electrical difference, which he attributed to periodic changes of the functional activity in the bulbar centres.

\* 'Untersuchungen über Thierische Elektrizität.'

† 'British Medical Journal,' 1875, also 'Transactions of the IX International Medical Congress, 1887.'

‡ 'Archiv für gesammte Physiologie,' PFLUGER, vol. 25, 1881, p. 281.

We commenced our researches in 1888, and published a preliminary account of the same as stated in the introduction to the present paper. Moreover, we demonstrated our method in 1889 before the Physiological Society, and further, at the International Physiological Congress, held in Basle, in September, 1889, we made a general communication on the method, and showed a complete experiment to the physiologists there assembled. An abstract of our paper in the 'Proceedings of the Royal Society,' was published in the 'Centralblatt für Physiologie,' 1889, and the account of the demonstration at Basle was published in October, 1889, not only in the 'Centralblatt für Physiologie,' but in the 'Progrès Médical,' 1889, and elsewhere. We have published, on the occasion of a priority discussion presently to be alluded to, in the 'Centralblatt für Physiologie,' 1891, the various publications we have made of our method arranged in chronological order. It was not until the close of 1890 that we learned that the galvanometric method was being employed abroad. On the 8th November, 1890, there appeared in the 'Centralblatt für Physiologie,' a paper by Dr. A. BECK, of Cracow, who, ignorant apparently of our publications and demonstrations, described the galvanometric method, and pointed out the value of it in determining the localisation of contripetal or afferent nerve function in the brain and spinal cord. This paper, however, was really but an abstract of a full paper which was presented to the Academy of Science in Cracow, in 1890, a copy of which we owe to the kind courtesy of Professor CYBULSKI, and in which is given a brief reference to the Basle demonstration, but no reference to our publications in 1888, or to Professor BIEDERMANN's abstract of the same in the 'Centralblatt für Physiologie,' 1889. The appearance of this paper produced a priority reclamation by Professor ERNST FLEISCHL VON MARXOW, of Vienna, published in the 'Centralblatt für Physiologie,' on the 6th of December, 1890. In this communication FLEISCHL showed that, as long ago as the 7th of November, 1883, he had deposited in the archives of the Imperial Academy of Science in Vienna a sealed letter, in which he announced that he had employed the galvanometric method for the same purpose, *vide infra*, as BECK and with the same details FLEISCHL, in this reclamation, does not mention any more than BECK, the prior investigations of CATON, or our publications and demonstrations of the last three years. Although FLEISCHL appears to have independently thought of employing the galvanometer as an index of functional activity in the nerve centre, when it is the seat of centripetal or afferent disturbance, his method of recording his idea in a sealed note, discounts the credit that otherwise might fall to him. All these authors have dealt with the employment of the galvanometer as an index of the changes going on in the nerve centre, *i.e.*, nerve corpuscles, when that nerve centre is directly connected with the instrument. We will allude directly to the results obtained by BECK and by FLEISCHL, but we wish to point out that from our own observations made in the same way, we are not at present satisfied that the basis of these researches is entirely trustworthy (see Chapter IX.), and that they deal with but one point in this extensive subject. So far as we are aware, we were the first to determine by use of the electrical

method the localisation and quantitative estimation of either centripetal or efferent impulses issuing from nerve centres in functional activity, and, in addition, we first employed it for the determination of the localisation of paths or channels of nerve function, particularly in the spinal cord. After this preliminary statement, which has been rendered necessary by the publications referred to, we will refer to the results which were obtained by FLEISCHL and BECK respectively, although, as we said just now, these results are, we consider, for the reasons we discuss on p 296, not to be immediately accepted. FLEISCHL (*loc. cit*) connected, by means of non-polarisable electrodes, two symmetrical points on the surfaces of the cerebral hemispheres with the galvanometer, and found that in the resting condition there was little or no electrical difference. If, however, a sensory end organ, whose corresponding area of the cortex was thus connected, were excited, the effect produced was an electrical difference as recorded by the deflection of the galvanometer. This effect he especially obtained when the visual centre discovered by MUNK was connected with the galvanometer and the eye illuminated, whereas little or no difference followed excitation of cutaneous nerve endings. Finally, he found that profound narcosis with chloroform or ether abolished this effect, and that special precautions must be taken against cooling of the preparations.

BECK (*loc. cit*) removed the brain, spinal cord, and sciatic nerve of the frog *en bloc* and placed the preparation on a glass plate, he then applied non-polarisable electrodes made of kaolin and 0.6 per cent salt solution to the longitudinal surface of the spinal cord and connected them with a Hermann's galvanometer. He found that there was constantly an electrical difference of such a nature that the centripetal, *i.e.*, proximal parts of the nervous system were always electro-negative to centrifugal or distal parts. If then the sciatic nerve were excited this primary difference was increased, provided the galvanometer electrodes were placed above the lumbar enlargement. If, on the other hand, the sciatic nerve were excited while one of the non-polarisable or leading-off electrodes were placed on the lumbar enlargement, there was observed a negative variation of the primary difference. In another series of experiments on Dogs and Rabbits he connected two points of the surface on one hemisphere with the galvanometer, and found that there were more or less regular swaying movements of the needle, and which he regarded as "action currents". Excitation of the retina caused the visual centre of MUNK to become negative to the rest of the hemisphere.

DANILEWSKY\* has quite recently published the results of five experiments which he performed in 1876, and in which he found that when non-polarisable electrodes were connected with the cerebral hemispheres (whether superficially or deeply) and with a sensitive du Bois-Reymond galvanometer negative variations of the resting difference were observable as consequences of various modes of sensory stimulation. The portion of the hemisphere from which these effects were obtained was the

\* 'Centralblatt für Physiologie,' April, 1891, p 1

posterior part alone, and in most cases opposite to the side to which the excitation was applied

### CHAPTER III—DETAILED DESCRIPTION OF THE METHODS EMPLOYED IN THE PRESENT RESEARCH

The description of the methods may be best effected by considering, in succession —

- 1 The method of anæsthesia employed
- 2 The operative procedure
3. The recording and exciting apparatus.
- 4 The general procedure and the precautions used

#### SECTION I—METHOD OF ANÆSTHESIA

The anæsthetic employed in these experiments was, in almost all cases, ether, the exceptional cases being those in which some bronchial or nasal catarrh rendered it advisable to substitute chloroform, this latter giving a more even and steady narcosis, though at greater risk to the animal

The physiological action of ether has received considerable attention lately, and a few points in connection with it are of sufficient importance as bearing upon our experiments to warrant a more detailed notice

In the first place, it has been shown (HOOPER, SEMON and HORSLEY, BOWDITCH, and others) that ether when present in the circulating blood through inhalation, appears to have a distinctly differential effect upon the two kinds (red and white) of muscle, or upon their innervation, *i e*, centres, fibres, or nerve endings

Further that the direct application of the liquid or vapour of ether to the trunk of a nerve causes paralysis of its physiological conductivity.\* (HOOPER and BIEDERMANN.)

The investigations of FLOURENS† in 1847 had elicited the fact that the inhalation of ether produced physiological effects, in which the functional activity of the reflex centres was abolished before that of the conducting nerve paths, and this has been substantiated by the work of other investigators.

It is with special reference to the action of ether upon these two structures that the present remarks are introduced, since, with the exception of the few experiments in which we employed the graphic method, our work has been entirely confined to the study of the changes in nerve centres and nerve fibres

It was consequently of primary importance for us to know to what extent the inhalation of ether has a differential action upon nerve centres as distinct from nerve fibres.

In this connection experiments (HORSLEY and SPENCER) have shown that the

\* BIEDERMANN, 'Wien, Akad Sitzber,' vol 97, 3 Abth., 1888

† FLOURENS, 'Comptes Rendus,' vol. 24, 1847, p. 161.

instant effect of ether inhalation is a remarkable fall in blood-pressure, such a fall in blood-pressure as the early experiments of VULPIAN showed would of itself, if sufficiently pronounced, cause a diminution in the functional activity of all the nerve elements, such diminution occurring first and most markedly in the centres, and even a comparatively slight fall may be followed by a loss in the excitability of these, although the nerve fibres might not be appreciably affected

The effect of ether, therefore, in diminishing the excitability of the cortex and lowering its functional activity may be in part due to changes in the circulation. It is probable, however, that the ether in the blood exercises a direct toxic effect upon the nerve structures, of a similar kind to that which is brought about by the direct action of the vapour already alluded to. We are not aware of any experiments as to the direct toxic action of ether vapour upon nerve centres, but it is extremely probable that such action occurs and that the centres should be affected by an amount of ether in the circulating blood which is too small to affect in any sensible degree the fibres.

Whatever the share which the two factors, blood-pressure changes and ether in the blood, may respectively have in the production of the effect, the result is that profound general narcosis serves to abolish the functional activity of nerve centres before that of nerve fibres. We have therefore made use of etherisation, with due caution, to assist us in analysing the compound excitatory effects observed when a complex structural arrangement of centres and fibres has been stimulated, and we have in all cases observed great care in noting as accurately as we could the degree, whether profound or slight, of narcosis at the time of each experimental observation.

There is one possible disadvantage in the use of large quantities of ether during a considerable period of time which is not very obvious at first sight, and that is the amount of vapour which is present in the air of the room. It did not occur to us that this could act injuriously upon the preparations under investigation until we noticed in three prolonged experiments in which, owing to the method of inhalation, a large quantity of ether was used in a warm close room, that both the exposed cortex and the sciatic nerve suddenly lost their excitability, which they did not regain. The possibility of this being due to that injurious action of the ether vapour dissolving in the liquids upon these structures, which was pointed out by BIEDERMANN, then occurred to us. The effect of the vapour in the room was increased, perhaps, by its dissolving in a warm bath containing 0.6 per cent saline, which mixed with the blood of the animal was employed for irrigation, &c, of the nerve structures. Although the failure might have been due to other causes (exposure, &c), still the fact of its not occurring when special precautions were taken to avoid the excessive evaporation of ether into the room and the contamination of the saline, leads us to conclude that the cause mentioned is at any rate a depressing factor which ought, as far as possible, to be excluded.

The use of chloral or morphia would undoubtedly entirely exclude any error of this



kind, but it has the enormous disadvantage that it is impossible to alter the degree of narcosis, and, as will be seen, such alteration is an essential condition in experiments of the kind which we have undertaken.

As regards the practical administration of the anæsthetic, the best results were obtained by pushing the etherisation at first to a profound degree, so as to abolish entirely superficial reflexes, and always by causing profound narcosis before performing any operation, such as division of the spinal cord, &c, which would, if the narcosis were less deep, entail depressant effects upon the centres concerned with systemic life through the damaging influence of shock. Subsequently when, the operative procedure having terminated, the actual observations were being made, the narcosis was rendered less and less intense as the slow collapse inseparable from the experimentation asserted itself. This slow collapse, since it involves the gradual failure in excitability of the nerve structures and primarily of the nerve centres, has the same effect as an anæsthetic in producing narcosis, which was preferably intensified by the administration of ether in small repeated doses rather than in few large ones.

## SECTION II — OPERATIVE PROCEDURE

### 1 *Exposure of the Cortex and of the Corona Radiata*

(A) *Cortex* — The animal, having been deeply anæsthetised in the manner stated, was further immobilised on a firm support, upon which a metal vessel was placed so as to be underneath the thorax. This was kept filled with hot water and, combined with suitable coverings for preventing loss by radiation, served to keep up the temperature.

The dura mater was then exposed *lege artis* to the necessary extent and over the required region, all hæmorrhage from the bone being instantly arrested by the use of soft modelling wax, &c. As soon as the dura mater was cleared the wound was closed, and kept covered with sponges soaked in hot 0.6 per cent saline solution, whilst the further operations necessary for the experiment were undertaken.

The cortex was finally exposed by taking up the dura mater by means of iridectomy forceps or fine curved needles, and dividing it, care being taken to keep it always protected with hot saline sponges unless an actual experiment was in progress.

(B.) *Corona Radiata* — The cortex having been thoroughly exposed, a sharp scalpel was passed horizontally through the hemisphere in the plane of the centre of the coronal gyrus, and the upper and anterior thirds raised as a lid of a box. Pieces of amadou were then gently laid and pressed on the edges of the cut, thus arresting the free bleeding from the vessels of the pia mater. Care was always taken to determine precisely the topography of the section, and to accurately apply the electrodes to the fibres coming from the requisite area of the cortex. The necessity



of this care is obvious to those who are familiar with the limitation of the fibres in the corona radiata, but we think it well to mention the fact, as a malposition of 2 mm is sufficient, with the stimulus we employed, to prevent the production of the effect

## 2 *Exposure of Peripheral Nerves*

The great sciatic nerve was usually selected for this purpose, and was exposed in the thigh for 6 centims. of its length. It was then divided near the knee, and its central end ligatured, care being taken to prevent any pull upon the structure, or any injury to the *arteria comes nervi ischiadici* which was always included in the ligature. When not required for purposes of immediate experiment it was irrigated with 0.6 per cent saline solution, and covered over by the skin and muscular flaps. During use, whether for purposes of excitation or in connection with the non-polarisable electrodes, it was always so fixed that no movement of the animal could pull upon the structure.

## 3. *Preparation of the Spinal Cord for Observation*

The spinal cord afforded naturally more difficulty in its preparation, and this requires therefore a more detailed description.

The objects in view were—

- (a) To expose and divide the cord.
- (b) To preserve as far as possible its circulation.
- (c.) To fix the spinal column so that no accidental movements of the animal should affect it.
- (d) To avoid the depression due to cooling, drying, &c.
- (e.) To secure for the purposes of electrical investigation as complete an isolation as possible of its different parts.

These requirements were met as follows —

(a.) *Exposure and Division* —The muscles were rapidly exposed over the dorso-lumbar region, and then partially extirpated and cleared from the vertebral laminae; hæmorrhage was treated by frequent irrigation with 0.6 per cent saline at a temperature of 50° C., and pressure of hot sponges. The exposed vertebral arches were then carefully removed piecemeal for 6 to 8 centims., by the aid of powerful but fine-pointed bone forceps.

In those cases in which the reflex effects of the lower fragment of cord were investigated, the cord was only exposed for a very short distance by the removal of one lamina and then divided under profound anæsthesia. The small wound was then closed and kept covered with hot sponges.

When a long portion of the cord was exposed the theca was divided in the middle line with great care, the division being especially free at that portion of the exposed area which was to remain in continuity with an unexposed region, so as to avoid

any danger of strangulation when the freed portion of cord was subsequently raised. On reflection of the dura, a ligature was cautiously passed around one end of the exposed cord, the end chosen varying in accordance as it was desired that the observed portion of cord should be in communication with the brain or with the sciatic nerves. If the former, then it was knotted gently round the lower end so as to securely close the vessels, and the cord divided immediately below the ligature. The (central) end was now raised by the ligature, and the nerve roots exposed and divided one by one until the whole portion of the exposed cord was freed from all attachment except at the upper end, where it was continuous with the central unexposed region. In the case of experiments upon the cord severed from the brain but in connection with the sciatic nerves, the ligature having been applied round the upper portion of the exposed tract, the cord was divided on the central side of the ligature and the exposed portion freed downwards in a similar manner to that just described.

(b) *Preservation of Circulation*.—The circulation in the exposed portion was maintained as far as possible by the ligature of its cut end, including the main vessels, and by keeping the cord in connection with an undisturbed portion, and avoiding any strangulation of that connection.

(c) *The Immobilisation of the Spinal Column*.—The fundamental importance of fixing the vertebræ necessitated the employment of a special clamp. This clamp was applied so as to firmly grasp in its powerful vice-jaws the transverse processes of the spinal column in the immediate neighbourhood of the exposed cord. The jaws were fixed on a stem, and approximated by an ordinary double screw. In order to avoid the extraneous electrical effects which the presence of metal surfaces in contact with moist cut tissues necessarily involves, the jaws were made of stout pieces of ivory. The stem carrying them was fixed to a powerful upright attached to the experimental table, and so arranged as to secure a fixation vertically above the preparation. (See Plate 29.)

(d.) *Cooling and Drying*.—The exposed cord was kept bathed with the warm saline solution until it was actually the subject of experiment, when, if it were raised in air, care was taken to keep steaming sponges in its immediate neighbourhood.

(e) *Isolation*.—The necessity of isolation for purposes of galvanometric observation will be referred to later on. This isolation was produced by raising the ligatured end of the exposed portion of cord, so that the portion swung in air without pulling upon its deep attachment. The electrodes, &c., were adjusted as described in the succeeding sections.

#### 4. *Division of the Exposed Portion of Cord by a Longitudinal Incision.*

For certain purposes it was desirable to observe the galvanometric effects in each half of the cord independently. These were (1) the determination of the comparative

value of the cord excitatory effect direct and crossed when the cortex is excited, (2) the determination of the bilaterality of representation in one hemisphere, and (3) that of the extent to which fibres cross from one side of the cord to the other.

We therefore devised the plan of dividing the exposed portion of cord by a longitudinal incision, either in the lateral or antero-posterior direction.

The former was effected as follows —

The cord, having been exposed, was severed, freed from its attachments, as previously described, but not ligatured. It was then kept bathed with warm saline, and placed upon a thin sheet of warmed cork with a shallow groove in it. The posterior fissure could always be easily seen, and a longitudinal incision was then carried through it from the posterior to the anterior fissure by means of a razor or sharp scalpel, the incision commencing at the attached end of the cord. It is essential that in this operation the instrument should neither pull nor press upon the cord unduly, but, since the division involves both pressure and pull, the infliction of injury can only be mitigated by slowly making drawing incisions, first only through the posterior fissure, and subsequently deeper and deeper until they have passed into the thickness of the cord. The exposed portion is partly divided in this way down to its point of transverse division for a distance of 2 centims or more. Irrigation with warm saline being maintained, the edges of the wound are gently separated, when the central canal of the cord will be seen in the bottom of the cut, with this as a guide, it is easy to continue by similar incisions the mesial division, until a complete separation of the cord into two halves is effected (See Plates 31 and 33)

Each half thus prepared was now ligatured close to its cross section, and raised in air for the necessary isolation when it was desired to subject them to electrical observation. They were kept apart by the ligatures being carried to the respective ends of a glass T-piece, or of two vulcanite rods arranged as a V.

Frequently the cord, when thus prepared, bled rather freely from the central end of the cut.

The simplest way to check this was found to be to press into the lips of the cut a small fragment of soft dry amadou, and leave it in contact with the bleeding point.

It might, perhaps, have been expected that such division would seriously impair the physiological conduction of its fibres. It will be seen in the following pages that, as far as the lateral tract is concerned, such impairment is not evidenced by our observations, but that undoubtedly the posterior columns in the immediate neighbourhood of the incision are injuriously affected by the process.

We have also divided the cord into a posterior and anterior half by gently raising it when freed and passing through it a thin-bladed knife from side to side opposite the attachment of the ligamentum denticulatum, and carrying it forward to the free end of the preparation.

### 5 *Preparation of the Spinal Cord for Excitation*

Another mode of preparation remains to be referred to, that, namely, in which the cord, when severed from its connection with the brain in order to investigate the functions of the lower fragment, is to be excited.

It was necessary for these experiments to sever the cord as high as possible, though, as a matter of fact, it was found advisable not to perform the operation at a higher level than that of the 7th dorsal vertebra, otherwise, serious impairment of respiratory and vaso-motor functions followed, and profound shock vitiated the experimental results. When the upper end of the lower fragment of cord was to be excited, this was further exposed, and a piece 5 mm in length excised on the peripheral side of the section, so that by looking into the gap the structures on the cut surface of the cord could be seen and the excitation localised. The gap was made absolutely dry with amadou and small pieces of sponge when the cord was to be excited.

Finally, a series of experiments involved the division of the cord at two levels. A portion was thus cut off, both from the brain and from the lumbar plexus, and prepared so that one end could be connected with the non-polarisable electrodes and observed whilst the other was excited. In all these cases the upper division was effected first, so as to diminish the shock which the further operative procedure connected with the lower division caused. The end with which it was desired to connect the electrodes was then carefully exposed, ligatured and freed from its connections, as already described under (3), whilst the other end was prepared for excitation.

### 6. *Preparation of the Roots of the Nerves.*

The posterior and anterior roots were in some instances prepared for excitation, in others for observation. In both cases the roots chosen were those forming the *cauda equina*, and they were exposed by a suitable opening of the spinal canal and theca in the manner previously indicated. The roots were carefully separated and when required each one was ligatured near its peripheral attachment and divided. Great care is necessary to avoid pulling, drying, &c., in the case of the roots. (See Plates 34 and 35.)

### 7. *Section of Columns of the Cord.*

In many experiments it was necessary to make a section of one or more of the columns of the cord between the part excited and the part observed. The method employed was to expose a portion of cord for the purpose and then to make the section by means of BEER's cataract knife, completing it by means of a fine-cutting needle or occasionally fine-pointed sharp scissors. In every case the limitation of the section was ascertained by *post mortem* examination. When a hemisection of the cord

was to be made, an additional precaution was adopted to ensure its accuracy, the cord being fixed by a fine needle

In some instances it was desirable that such intervening localised sections\* should be made some weeks previous to the actual experiments. This notably increased the labour of the research, but is an essential control to such an experimental enquiry as the present one. The animal was in all instances etherised and the seat of operation having been carefully shaved, disinfected, &c, the necessary exposure and section were then made under all aseptic precautions, the wound uniting by first intention when treated in the manner described by one of us in previous experiments of this kind.

In conclusion, it may be pointed out that since almost each experiment involved exposure, &c, of several different portions of the central nervous system, we adopted the plan of performing these slowly, taking at least an hour or more in the preliminary operative part of the experiment. We found that in this way less general shock occurred than when the various parts were rapidly prepared one after the other.

### SECTION 3 —RECORDING AND EXCITING APPARATUS

The recording and exciting apparatus used in the present research was chiefly that adapted for determining the comparative amounts of the electrical changes in the spinal cord and nerves at rest and when subjected to an excitation of definite intensity and duration.

The apparatus and its arrangement will be best indicated by separating it into the following groups.—

- (1) The apparatus used in connection with the observation of the electrical changes.
- (2.) The apparatus used in connection with the excitation.
- (3) Extra apparatus used for determining the characters of the muscular contractions.

#### 1 *The Electrical Apparatus for Observation*

Both these instruments were used to indicate the electrical changes evoked in the spinal cord and nerves.

(a) The *capillary electrometer* was made by Mr G. J. BURCH†. The mercurial column was magnified about 300 times by the special microscopic arrangement employed, and was sufficiently sensitive to show perceptible movements when connected with a difference of potential of  $\frac{1}{10000}$  Daniell, its reaction was quick enough to enable it to respond to a difference of  $\frac{2}{1000}$  Daniell when connected with that

\* The localisation of all points or regions of the cord exposed is expressed in terms of the body of the vertebra, or intervertebral disc, opposite to which the section was made. We furnish in Appendix A the topographical relations which the spinal segments bear to the superficial origins of the several nerves from the spinal cord.

† Proceedings of the Royal Society

difference by means of a rheotome for only  $\frac{1}{1000}$  second. The ocular of the microscope was fitted with one of ZEISS'S micrometers, the scale being worked across the field by a screw mechanism. In the particular arrangement employed, the scale bore such a relation to the actual dimensions of the capillary that one division corresponded to  $\frac{4}{1000}$  millimetre of the object. A difference of potential of  $\frac{1}{1000}$  Daniell when connected with the poles of the electrometer produced a movement of the mercury amounting to  $\frac{2}{100}$  millimetre, and this, when viewed by means of the eyepiece, amounted to five divisions of the scale.

The element of uncertainty in connection with the movement of the electrometer under different conditions and the difficulty of obtaining reliable records of changes differing from one another by constant but small amounts, induced us to abandon the instrument for the quantitative observations which make up the bulk of the present research. It was, however, often used as a means of ascertaining the existence and character of electrical changes during the initial stages of a new series of experiments, and proved in this respect a useful guide.

The movements of the meniscus were in most cases observed by the eye, but in some cases they were photographed upon a travelling sensitive plate, as in the experiments described in our previous publication.

(b) The *galvanometer* was the instrument upon which we relied for results susceptible of quantitative comparison. It was made by Messrs ELLIOTT upon the lines of THOMSON'S reflecting instrument, and had a resistance at 16° C of 20,364 ohms. The light magnetic system was effectually damped by being enclosed between two plates of glass 2 mm apart, the aluminium vane of the ordinary Thomson being dispensed with to secure a decrease in the inertia of the system.

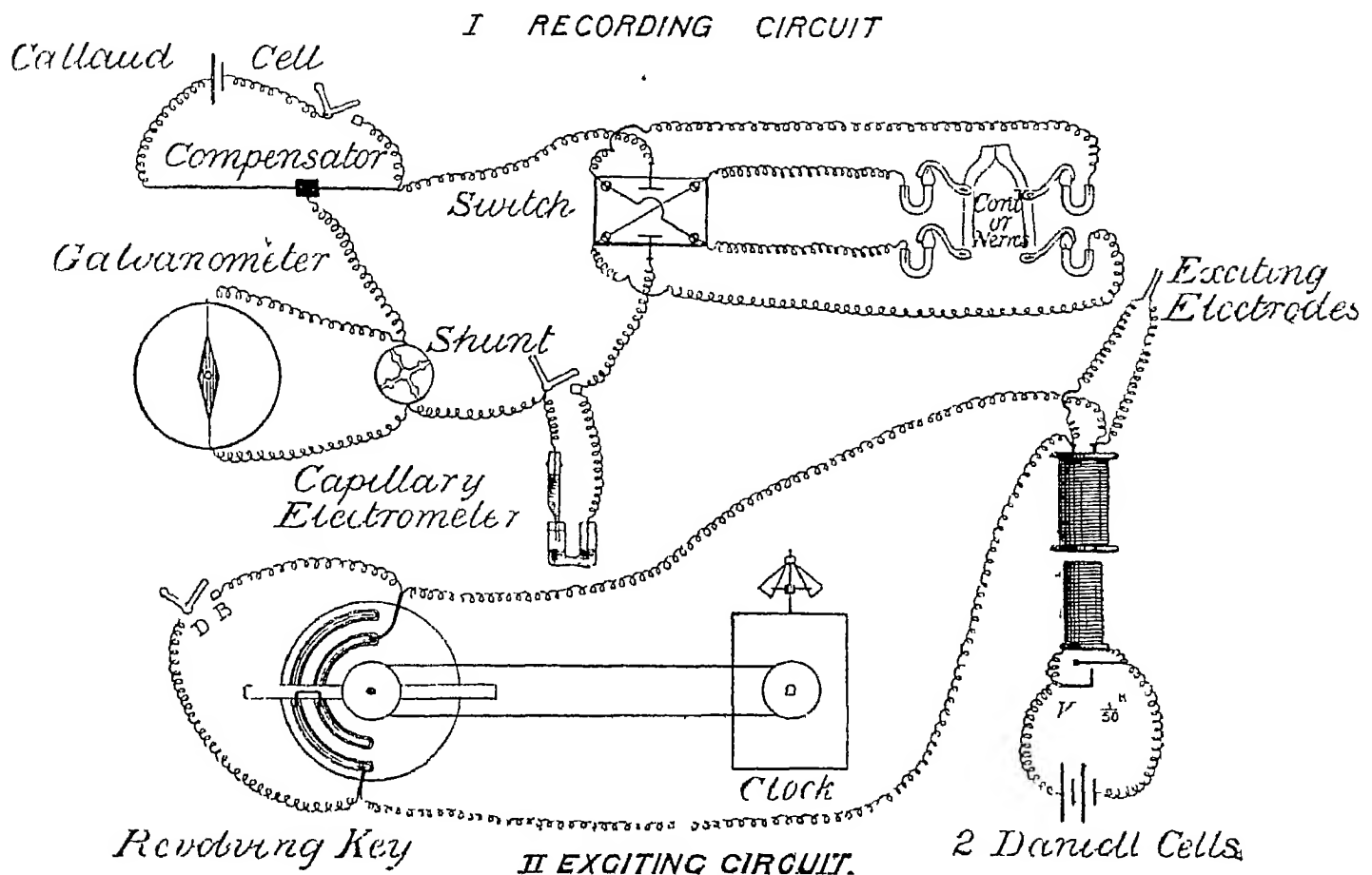
The degree of sensibility employed was such that the needle and mirror gave a deflection amounting by the reflecting method of observation used to 650 scale, when the instrument was connected through a resistance of 10,000 ohms (external to its own resistance) with a difference of potential amounting to .01 Daniell, and when only  $\frac{1}{100}$  of the current in the circuit was allowed by the shunt to traverse the instrument. The small mass of the system enabled it to respond to currents of very short duration, thus with an additional resistance of 10,000 ohms in the circuit, a difference of .01 Daniell produced a deflection of 5 scale when connected by means of a rheotome with the galvanometer for a period of only  $\frac{1}{1000}$  second.

The deflections of the magnetic system were measured by the usual reflecting method; a biconvex lens of 4 inches focal length was, however, introduced almost 3 centims. in front of the source of light between it and the concave mirror (of 40 inches radius) of the system. The screen behind which the light was placed was pierced by a circular aperture bisected by a vertical cross wire, and the reflected image on the scale was thus a large well-illuminated disc with a sharply-defined vertical shadow dividing it. The position of the edge of the vertical shadow on the scale could be thus observed with great accuracy, since the moving illuminated disc



was of sufficient size to embrace in its field a considerable range of the figures of the darkened scale on each side of the shadow of the upright.

Fig 1.



The arrangement by which either of the above-described instruments could be connected with the experimental circuit, and thus with the particular structure, whether spinal cord or nerve, under investigation, is shown in fig. 1.

In the above arrangement the method of compensation and the method of connection with the tissues call for a few descriptive details.

(c) The *compensator* was of the pattern used in the Physiological Laboratory, Oxford, and was similar in its general plan to that described by BURDON SANDERSON, as used in his work on the electrical properties of *Dionæa* \*

The total amount of wire in the instrument offered a resistance of 10 ohms, of this a portion at one end, 125 centims in length and of 1 ohm resistance, was exposed and lay tightly stretched upon a boxwood scale. Upon this boxwood bed a heavy block carrying a wire was allowed to slide. The block was furnished with a pointed index, the under surface of which, covered with platinum, formed the sole contact with the wire; its position was easily read upon the scale beneath it.

The battery used in the primary circuit of the compensator was the Callaud pattern, which is a Raoult battery without any porous cell. This had been found by one of us to be the simplest and most satisfactory battery for the purpose. As used in the present research, it consisted of a glass jar containing about a litre, into this

\* 'Phil. Trans.,' 1882.



about 300 grms. of sulphate of copper crystals were placed, and the whole filled up with distilled water, a coil of sheet copper, with insulated connections, is immersed in the crystals, and a ring of zinc in the superficial liquid

The cell was always prepared forty-eight hours before use, and since the subsequent alterations take place with great regularity and are slowly produced, the cell, when evaporation is prevented, is very steady, and is thus particularly suitable for the purpose indicated.

The value of a given interval between different points of the compensator wire when the Callaud cell was coupled up with it was always estimated before each experiment and contrasted with that produced by a known fraction of a carefully prepared Daniell cell. This latter was determined by the balancing method employed by DU BOIS-REYMOND and described by him in connection with his use of the "Rund Compensator" in his standard work on the technique of physiological experiments involving observations of electromotive changes. The measurements by the compensator, although made with the Callaud, were thus all translated into terms of a Daniell cell.

(d) The *non-polarisable electrodes* which formed the connection with the tissues consisted in some instances of two pairs. Each pair was then joined to the two screws on one end of a Pohl's reverser (without cross-wires) to the middle screws of which the wires forming the main circuit were connected. Either pair of electrodes could thus be rapidly connected with the recording instrument by turning over the switch. In this way the changes in each of the two prepared sciatic nerves, or in each separated half of the isolated and longitudinally divided cord, could be ascertained one after another in rapid succession.

In the majority of experiments only one structure was examined, and one pair of electrodes was therefore used and introduced into the main circuit.

Each electrode consisted of a U-shaped glass tube containing a saturated solution of zinc sulphate with a well amalgamated and annealed zinc dipping into one limb. This form was preferred in consideration of the experimental necessity of keeping the electrodes exposed for an hour or more, in order to minimize the alterations due to evaporation.

It was of the first importance that the connection of the electrode with the investigated structure should be so firmly attached as to suffer no displacement from any chance movement of the animal, and that they should be of such a nature as to readily permit an adequate isolation of the structure from all its neighbouring tissues. This was effected in the case of each electrode by means of thread cables made out of the soft strands of such wicks as are used in ordinary paraffin lamps, since these readily imbibe and become soaked with moisture. Two strands 10 centims long, were usually taken and soaked in 0.6 per cent. solution of NaCl, they were then plastered with powdered kaolin, made into a paste in similar liquid, and thus united into a double cable. This cable was passed under the structure investigated and tied gently

round it; the two ends of the tie were then united together, thus forming a cable of four strands. The end of this cable was fixed into a plug of kaolin moistened with similar sodium chloride solution, which was united in the usual way with sulphate of zinc kaolin paste, and this with the liquid in the one end of the U-tube. Since from 4 to 5 centims of this yielding cable thus hung between the rigid part of the electrode and the attached structure, this latter could be moved so as to isolate it from the neighbouring tissues without interfering with its electrode connection, whilst, owing to the soft cable being tied around the structure no displacement of the point of contact was possible in consequence of such movement.

## 2. *The Exciting Arrangements*

The method of excitation involved the use of (a) electrical, (b) mechanical, (c) chemical stimuli. Of these the electrical, as alone admitting of accurate graduation, is the most important.

(a) *Electrical Excitation* —The exciting arrangement involved in almost all cases the production of a rapid succession of induction shocks. These were obtained from the secondary coil of an induction apparatus of the general pattern of that devised by DU BOIS-REYMOND, and usually employed in physiological research. The particular coil used was made and standardised in Berne, under Professor KRONECKER's direction, and differed from those ordinarily used in having a scale which denoted for every position of the secondary coil, with reference to the primary, the relative intensity of the current induction effect (BOWDITCH.) Since the ordinary scale, that of distance in centims. is most generally known to physiological workers, we append the comparison of the numbers of the two systems showing their relative intensity.

### Du Bois-Reymond inductorium scale

	cm	0	1.	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22.	23	24	25
Divisions of Kronecker in- ductorium scale		13,000	12,500	12,000	11,250	10,270	9,250	8,500	7,300	6,300	5,300	4,300	3,300	2,400	1,700	1,000	600	420	300	250	180	130	87	70	58	48	41
																	Fraction over										

Two Daniell cells coupled for intensity were used in the circuit of the primary induction coil; this contained an automatic electro-magnetic vibrator, which closed and opened the circuit 50 times per second.

The interrupted circuit was a derivation bridging the primary coil (Helmholtz side-wire), so that each interruption should induce make and break currents of approximately equal intensity, thus avoiding the accumulation of polarisation after-effects in the excited tissue. The electrodes were well insulated platinum wires with points 1 millim. apart. When placed on the tip of the tongue, a slight acidity only was

perceptible with the secondary coil at 2000, the tingling effect becoming first distinctly felt at 4000, and painful at 12,000.

The arrangement of the exciting circuit is given in the preceding figure 1, p. 289, the only feature calling for remark being the use of a revolving mercurial key in the secondary circuit

This key consisted of a hard paraffin bed, supporting two semi-circular narrow vulcanite troughs containing mercury. Into these dipped the two ends of a loop of stout platinum wire, which was carried by a horizontal revolving vulcanite arm. Each mercurial pool was connected with one terminal of the secondary induction coil, so that when the platinum loop connected the two pools a short circuit was made for the secondary coil. The arm was driven by a clock at such a rate that a whole revolution occupied a period of 10 seconds

By means of the key (*DB*) shown in the plan, the secondary coil was additionally short-circuited, and the revolution of the arm thus made ineffectual, when, however, it was desired to excite the preparation, the key was opened for one revolution only, and the secondary coil was thus disconnected from any short circuitous arrangement during 5 seconds. The interrupted induction currents were thus allowed to traverse the tissue between the platinum points of the exciting electrodes for this period only.

(*b.*) *Mechanical stimulation.*—The importance of obtaining evidence of physiological effects by different methods, as a control to the definite results obtained with electrical excitation, led us to employ mechanical stimulation wherever practicable. The simplest form of mechanical stimulus, and the most effectual, is undoubtedly that obtained by the complete and sudden severance of a tract of fibres. This we accomplished, when the position of the parts allowed of it, by the use of sharp scissors, thus severing, for instance, the sciatic nerve, and observing the electrical change which the division evoked in the spinal cord, and *vice versa*. As, however, in some cases the metal blades of the instrument coming into contact with the moist tissue caused localised electrical changes, derivations from which affected the galvanometer and electrometer, we substituted the stimulus occasioned by the sudden tightening of a ligature, and also that caused by crimping the tissue, nerve, or cord, by squeezing it suddenly (sometimes so as to divide it) between the jaws of a pair of specially constructed ivory scissors

The method of stimulus being used only as a control, the disadvantage of few repetitions being possible was not a serious one.

(*c.*) *Chemical Excitation.*—In addition to the previous methods of excitation, we have made use of strychnia, in intraperitoneal injections, in order to obtain pronounced reflex discharges from the spinal cord.

Further, we have frequently employed, with notable advantage, the method of exciting the brain first investigated by MAGNAN, viz., the production of nerve impulses from central apparatuses by the toxic influence of certain substances, especially the essence of absinthe

Just as the mechanical stimulus affords, perhaps, the best control of the electrical stimulation of fibres, so the chemical, since it excites centres powerfully, affords a means of producing electrical changes in the efferent fibres from such centres which cannot possibly be due to actual escape of the exciting current.

For the performance of this method we have prepared the cord or nerve for connection with the non-polarisable electrodes as described previously, and then exposed for a short distance the external jugular vein, applying a small clip to the latter.

Two minims of the essence of absinthe were then injected with a hypodermic syringe inserted through the vein wall into the freely flowing blood stream

The animal was then carefully observed and the first twitching indicating the commencement of a cortical discharge noted. It coincided in time with the beginning of large electrical effects as evidenced in the galvanometer. For further facts relating to this method we would direct attention to the Chapter dealing specially with the results thus obtained, *vide* p 511

### 3 *Extra Apparatus*

The apparatus used for investigating the muscular changes evoked by excitation of the central nervous system was either adapted for a direct record of the character of the muscular contraction or for ascertaining the moment of its commencement.

When necessary the muscular contractions, whether evoked by cortical or spinal excitation, were recorded by means of a spring lever, made on the pattern of that employed by FICK for obtaining isometric muscular effects. The muscle was attached so that any changes in its tension were communicated to the spring, the small movements of which were magnified fifty times by a lever attached to its end. The lever recorded its movements on the blackened paper of an ordinary drum driven regularly by a clock.

When it was desired to ascertain the moment of the commencement of the muscular contraction, however evoked, the method employed by TIGERSTEDT was used. The Mammalian muscle was attached to the light "*unterbrecher*," which carried a weight of 10 grm. placed upon its axle, to ensure a steady pull upon the large muscle and a proper tension of its attachment. The *unterbrecher*, as in TIGERSTEDT's method formed a key in a separate circuit, which included a battery of three Grove's cells and one of SMITH's\* new electromagnetic signals. The break of the key and the consequent movement of the signal was recorded upon the glass plate of a spring myograph (DU BOIS-REYMOND's *Federmiographion*) which travelled at a rate of 2 centims in  $\frac{1}{100}$  second.

\* 'Philosophical Magazine,' 1889.

## SECTION 4 — THE GENERAL PROCEDURE AND THE PRECAUTIONS USED BY THE AUTHORS

### *A The Method of Experiment*

In any individual experiment in which excitatory electrical changes were observed the procedure we adopted was as follows —

The animal having been anæsthetised and immobilised, the structure to be investigated was exposed and prepared in the manner indicated. It was always, whether spinal cord or nerve, divided, and the soft cables of the non-polarisable electrodes were then tied, one round the structure close to the point of division, the other about 1 centim away round the surface. The ligature upon the cut end enabled this portion of the tissue to be suspended with its cables in air, without dragging on the remaining portion of the tissue which remained *in situ*. The cables were then connected with the non-polarisable electrodes. (See Plate 29.)

The electrical difference between the two contacts was first observed and balanced by the introduction by means of the compensator of a suitable difference opposite in sign to the tissue difference. The general characters of the latter and the amount of the balancing difference were then noted, both the galvanometer and electrometer being used for this purpose.

One of us devoted himself to the observation and record of the electrical changes, the other to the maintenance of the animal in a uniform condition of anæsthesia, to the prevention of the drying, &c., of the investigated tissues, to the observation of the muscular contractions, and to the excitation.

The tissue to be excited, which had been exposed with that under investigation, was then finally prepared, and the points of the electrodes were brought into contact with it under all the precautions to be immediately described.

The electrodes were kept short circuited as already stated by means of a key under the control of the observer at the galvanometer, &c. When everything appeared favourable and the galvanometer needle had been brought to its zero position by suitable compensation the revolving exciting key was set going and the control key opened for one revolution of the revolver, an excitation of definite duration and intensity was thus applied to the excited tract, whether cortex, corona radiata, spinal cord, or nerve. The extent of any deflection of the galvanometer needle or the movement of the meniscus of the mercurial column was noted, and special attention paid to its character. The extent recorded was always that between the previous resting position and the point where the moving recorder, whether spot of light or image of meniscus, stopped and commenced its return. If no return occurred but only a deflection produced which continued to creep on then the observation was disregarded as worthless. Such an effect was found to be generally associated with some movement of the animal which caused a slight displacement of the electrode contact.

Whilst one observer noted the electrical effect, the other noted the extent and character of any muscular movements by which the animal responded to the stimulus

It need scarcely be said that the whole method involves the use of special precautions to avoid the introduction of fallacious and misleading effects, especially when it is desired to obtain a succession of results which will admit of quantitative comparison

These precautions are, in the opinion of the authors, of the utmost importance and must be considered in some detail

### *B. Precautions in Connection with the Method.*

The special precautions may be grouped as follows —

- (1.) Those connected with the isolation of the particular region under observation
- (2) Those connected with the condition of the non-polarisable electrodes
- (3) Those connected with the condition of the animal.
- (4.) Those connected with the localisation, &c., of the excitation

#### *(1) The Isolation of the Particular Region Observed.*

It is, in our opinion, an essential condition for the accurate employment of any method of localisation which relies upon the evidence of electrical changes in a given region, that the region in question should be as far as possible isolated. In the galvanometric experiments alluded to in the History (p 279), as carried out upon the cerebral hemispheres, such isolation was not affected; a door was thus left open for introduction of errors which it is not easy to control.

We have repeatedly had occasion to observe that when a pair of non-polarisable electrodes is placed upon the cord lying *in situ*, or upon the surface of the exposed brain (see fig 26, Chapter XI) electrical differences present themselves and influence the galvanometer, this being evidently due to the fact that the parts with which the contacts are made, since they form one directly continuous mass with the structures around them, lie in the path of the derivations of currents, whose primary electromotive source is far removed from the electrodes

In this connection we may refer to the derivations of the electrical difference between the different regions of the beating\* heart which are present in the body

On connecting two points on the surface of the exposed brain by means of non-polarisable electrodes with the galvanometer, any reflex movement of the scalp muscles lying outside the exposed region was found to evoke electrical changes in the points of contact, and if structures so far removed from the seat of observation can affect the contacts, how much more easily will these be affected by sources of electromotive differences situated in the deeper fibres, &c., of the brain. The fact that electrical

\* WALLER, 'Phil. Trans.'



changes manifest themselves between two surface contacts is thus by itself no proof that these electrical changes have their source in the tissue in the immediate neighbourhood of the contacts. It is, however, easy to ascertain whether the opposite conclusion is or is not true, by slicing off the two portions of the surface to which the electrodes have been attached, destroying their vitality, and replacing them in contact with the subjacent tissues, so as to act as mere moist conductors. If under these circumstances electrical changes are observed in the electrode areas, then it is clear that since all structural and physiological continuity is destroyed, these changes must be due either to (1) physical properties of the observed region, which are in no way associated with physiological vital changes; or (2) to the physical spread of derived currents from electrical changes of physiological origin in the deeper uninjured tissues.

The further distinction between these two alternative causes is effected by observing to what extent the electrical changes disappear in consequence of systemic death, since this obviously will affect the second class but not the first.

It is, in our opinion, essential in all exact experimental investigations carried out upon a particular region of such a mass of conducting material, as the body of an animal constitutes, to use a method which can by strict investigation carried out along the above lines be shown to exclude such discrepancies.

It may be pointed out that whilst we have selected the brain mass as a typical instance, the same objections apply with equal or greater force to the investigations of the spinal cord *in situ*. When it is remembered that the exposed cord lying in its cavity is brought into immediate connection with a large mass of muscles, some uninjured, some cut for operative purposes, and with the whole contents of the abdominal and thoracic cavities, it is not to be wondered at that the slightest movement of the animal should cause very large electrical changes between any two portions of the surface of the exposed cord, these being simply due to an alteration in the position of muscles or other structures, all of which are the seat of electromotive change. Such alterations must seriously influence the particular effect which may manifest itself when any two portions of the exposed cord are connected with the galvanometer. The force of these considerations is strengthened when it is borne in mind that the particular effects which the electrical method is to gauge, are excitatory in character. Of what value would any excitatory effect be, if, when it is evoked, there are, as is almost always the case, not only marked excitatory electrical changes in other organs, muscles, &c, but general movements and displacement of subjacent parts as the result of the excitation?

Enough has now been said to point out the necessity for the utmost possible isolation of the observed region, if it is desired to ascertain by the electrical method the presence of electrical changes due to electromotive differences occurring in that region only, and which may be therefore interpreted as indicating the presence therein of excitatory conditions.

The most complete method of isolation is obviously the removal of the structure



under observation from all contact with other tissues. This is not possible in the case of the Mammalian central nervous system, it is, however, quite feasible in the case of the spinal cord to ensure an isolation which we find to be sufficient. This, as has been detailed in the section dealing with the operative procedure, as regards its essential feature consisted in always dividing the cord, freeing it for several centims from all its attachments, ligaturing the divided end, and suspending this portion in air by means of the ligature (see Plate 29) The cord is thus only in connection with the structures by its deep end, and any spread of electrical currents, &c., which have their source in extraneous regions, can only occur in this portion of cord as "extrapolar effects", further, the electrodes being placed one upon the extreme end (cross section), the other only half to one centim on the proximal side of this, such extrapolar derivation effects, if present, must be still more diminished by the distance, 3 centims, between the electrode contacts and the deep connections of the cord

The necessity of the above careful isolation has been impressed upon us by the ease with which it is possible to introduce errors even where this mode of connection is carried out. If, for instance, either the proximal contact be allowed to slip down and to approach too closely (within 1 centim or less) to the deep structure, or if the latter, by the presence of large quantities of liquid, &c, be brought into connection with a portion of the isolated tract close to the proximal electrode, then, even with the remaining electrode contact well isolated, electrical effects manifest themselves between the contacts, which we have no doubt are really due to extrapolar spread from changes in the deeper tissues. Thus, for instance, the anterior roots, even when divided and one end isolated, present great difficulties, owing to the shortness of the tract intervening between the contacts upon them and the cord from which they spring. Electrical excitatory effects can be obtained on exciting the brain, which are apparently situated in the anterior roots, but which are in this arrangement largely due to electrical changes, situated in the cord, and occur as extrapolar derivations in the anterior root. This is readily proved by using the method of control previously referred to, viz, cutting off the attachment of the root to the cord and then replacing it in its old position, when, in spite of the want of structural and physiological continuity, the changes are still found to occur.

We cannot lay too much stress on the necessity of careful isolation as far as practicable, and of careful investigation by both the methods indicated, and other similar ones, of the extent to which observed electrical effects are due to mere physical spread through the moist tissues of changes in other regions than the observed ones.

It will be understood, therefore, that in the following experiments, when the cord or sciatic nerve was observed, the length of the tissue afforded every facility for placing the electrode connections at a safe distance from the point where each of these structures came into relation with the general mass of the body, and in consequence a position could be chosen in which all danger of extrapolar spread might with ordinary care be guarded against. When, however, the roots were observed, since

the distance in question was necessarily short, the dangers of extrapolar spread were increased, and the experimental results had to be controlled with great care; this danger was most formidable in the case of the anterior root, as owing to its anatomical relations it could not be so conveniently separated from its contiguity with the mass of the cord, and the errors thus introduced have been at present sufficiently serious for us to abandon these roots for direct connection with the galvanometer, and rely on those experiments performed upon the sciatic nerve with all the posterior roots cut

## (2) *The Condition of the Non-polarisable Electrodes*

It is scarcely necessary to observe that one obvious precaution in connection with the electrodes is to ascertain, before commencing the experiment, that between the electrodes themselves there is only an extremely slight and constant electrical difference, and noting its amount in terms of the compensator

There is one difficulty, however, which appears to be inseparable from a method which involves a long bridge of kaolin moistened with 0.6 per cent of saline, exposed to the air of the room, and that is the alteration of resistance due to slow evaporation. This alteration does not affect the results when observed by the electrometer, owing to the very high resistance offered by the latter. It may, however, seriously affect the galvanometer results. It will be obviously mitigated by employing a circuit of very high resistance, and this we always took care to do, the full resistance of galvanometer and electrodes amounting to little short of 50,000 ohms

It is, however, necessary to keep in mind the presence of such alterations, and to ascertain by repeated measurement of the galvanometric effect produced by a given difference in the compensation circuit, whether the resistance has so altered as to vitiate the value of the results. Where experiments follow one another closely, as was the case in all the instances in which the different columns of the spinal cord were excited, any alteration would be obviously too slight to exercise an appreciable influence upon the results, which admit, therefore, as far as this feature is concerned, of strict quantitative comparison

It is obvious that remoistening of the electrodes must only be effected at the commencement of a fresh series of observations, and must on no account take place during any given series

## (3.) *The Condition of the Animal.*

(a.) *General Preliminary Condition*—In all the experiments this was a very important factor, which we early recognised as determining the success or failure of the particular observations. If the animal were ill, or had been much exhausted by the preliminary anaesthetisation, &c., it was noted that the electrical changes, whether due to currents of rest or of action, in both nerve and spinal cord were comparatively small in amount. This was especially the case in the Monkey.

(b.) *Anaesthesia*—The degree of narcosis is an extremely important factor. It will

be seen in the chapters which deal with the different groups of results, how the effects obtained in slight anæsthesia differ from those obtained with similar stimulation in profound narcosis. It was, therefore, extremely important to keep the condition of anæsthesia as far as possible even, and to note as a guide to that condition the presence or absence of muscular movements, when any part of the central nervous system was stimulated

In one respect, the degree of etherisation was most useful, since it served as a valuable control against error due to simple electrical escape from the exciting into the galvanometric circuit. It is evident, if on pushing the degree of narcosis the electrical changes in the observed tissue are very much diminished or even abolished, whilst the excitation by electrical current remains unaltered, that no physical conduction of derivation currents from the exciting into the galvanometric circuit can be present

(c) *Collapse*—Since the experiments are often necessarily spread over a considerable period of time, the gradual collapse of the animal is not infrequent. Its onset is readily distinguished, and can be allowed for by diminishing the amount of etherisation (see p. 282), and by increasing the intensity of the stimulus used

(d) *Hyperexcitability*.—In connection with this part of the subject must be noted the variations in excitability of parts due to section

As regards the cortex it has occasionally happened that it has been slightly punctured by an electrode point, &c. Whenever this happened the effect was to heighten the excitability of the immediate neighbourhood, and to produce thereby a very marked epileptogenous change. A more extensive injury has the further effect of abrogating not only this increase of excitability, but the normal degree as well

As is well known, the excitability of nerve *fibræ* is raised by their section, and from a rapidly attained acme the excitability steadily diminishes, passing the normal point and becoming subnormal. FRANÇOIS FRANCK has shown the same to be true for the reflex centres in the spinal cord, when division of the latter has been carefully made high up and without notable hæmorrhage. We have always borne this in mind, and have discounted the rise and fall of excitability due to the section in each observation

#### (4) *Localisation of the Excitation, &c.*

Many precautions had to be observed in carrying out the stimulation of the cortex, spinal cord, and nerves respectively, especially when the excitation of these structures was electrical

A *Cortex*—As previously stated, it was, of course, found imperatively necessary to keep the surface of the cortex both warm and moist, this being especially achieved by replacing the skin and by irrigation with warm saline solution. To avoid short circuiting and consequent irregular intensity of the exciting stimulus, the surface of the brain was always carefully dried with soft sponge or amadou immediately before

the application of the electrodes. Fatigue of the cortex was avoided by suitable intervals of rest.

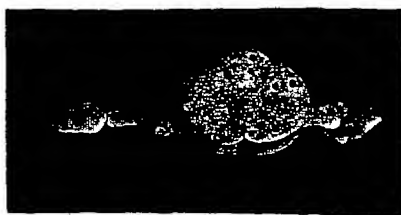
The intensity and character of the stimulus is referred to under apparatus, p 291, but it may be here stated that the electrodes were fine platinum points 1 to 2 mm apart.

B. *Corona Radiata*—To expose the corona radiata it was necessary to raise the cortex by a horizontal incision, and then to check the bleeding from the pial vessels with pieces of amadou around the cut border of the area exposed. If after several excitations the exposure had lowered the excitability of the fibres, the electrode points were sometimes inserted 1 mm deep into the substance of the corona, instead of, as usual, resting gently on the surface. The electrodes employed were the same as those for the cortex.

C *Spinal Cord*—The excitation of the spinal cord, especially for purposes of differentiation of the columns naturally demanded special attention. We obtained our initial generalisations by means of exciting needles fixed on either side of the cord or pressed against the longitudinal columns, *vide* pp 369, &c.

This method we soon discarded (Section 6, Part V,) for that now to be detailed, *viz*, the excitation of the cut sections of the columns of the cord, inasmuch as the differentiation of the bundles of fibres could thus be accomplished at the same time as other objects in view. The cord having been previously divided in the manner stated above, and the surface and surrounding tissues being carefully dried, the fine platinum electrodes, 1 mm. apart were used. It was our aim to provide for the excitation of as many fibres in any column as possible in order that the largest galvanometric effect might be evoked, and at the same time to avoid extrapolar excitation of neighbouring columns. These particulars were fulfilled by applying the two electrode points, as indicated on the accompanying fig 2, *i.e.*, vertically on the anterior and posterior columns, and horizontally on the lateral column in the region of the crossed pyramidal tract.

Fig 2



Photograph of a transverse section of the fresh spinal cord (Cat) at the 7th dorsal nerve, slightly magnified. The remarkable differentiation of the posterior columns in this animal (SCHIFF) is well seen.

That these measures were effectual in localising the stimulus was demonstrated by the fact that the placing of the electrodes on the neighbouring sections of the grey columns evoked no electrical changes, as evidenced in the galvanometer connected either with the issuing nerves or with another portion of the cord, so that the

positive electrical results following stimulation of a column, the posterior, for instance, were to be attributed entirely to the localised stimulation of the structures upon which the points of the electrodes rested

A further point is the special difficulty of maintaining the electrodes properly in position, *i.e.*, in contact with the cord, inasmuch as the spinal muscles on their contraction shake the cord a little, although the spine be fixed. This, of course, applies only to the end excited. Imperfect apposition of the electrodes was best avoided by holding them in the hand, the latter being suitably supported. As is described on p 292, the duration of excitation was provided for by the revolving mercurial key, consequently, after the proper contacts had been made as above, each observation was comparable with another as regards the degree of the excitation. The important bearing this has on the quantitative value of the galvanometric readings is sufficiently obvious

*D Nerve*—In electrical excitation of the nerve, we were chiefly anxious at first to avoid possibility of spread. Beginning with ordinary sheathed electrodes, into which the sciatic nerve was laid, we very soon laid these aside for the more accurate and simpler plan of applying platinum electrodes to the nerve raised in the air by a thread.

The mode of exciting a nerve in relation to its cross and long diameter respectively, has for some time been the object of research (HERMANN, BERNSTEIN, and others) GAD,\* in referring to the action of carbonic acid, and especially of alcohol, on the excitability and conductivity of nerve fibres, raises this question again, and strengthens the fact that transverse excitation is much more adequate (5–6 times) than stimulation applied longitudinally. Apart from incidental polarisation it is clear that the larger number of fibres lying in the principal axis between the poles chiefly conditions the result

To produce a maximal effect we have, therefore, always applied the platinum electrodes, so as to bend the nerve slightly between the terminal points (See fig 3)

Fig 3.



Inasmuch as we always sought to obtain, with as weak an excitation as possible, a maximal effect for purposes of quantitative as well as qualitative comparison, it was especially necessary for us to excite, without fail, all the fibres in the nerve

The usual method of simply placing the nerve on the electrodes, as, for instance, in using sheathed or hook patterns, only enables a few fibres to be excited—those immediately in contact, or nearly so, with the metal. Thus, BEEVOR and HORSLEY†

\* 'Archiv fur Physiologie,' (DU BOIS REYMOND) 1889, p 350

† 'Roy. Soc. Proc.,' 1888

have seen differentiation of a mixed nerve on applying the electrodes to one or other side of the trunk of the hypoglossal above the descendens noni branch

We have, of course, found that great differences are produced according to variations in the condition of the Mammalian nerve under varying circumstances

The nerve must not be dragged upon in any way and the electrodes must be in good *moist* contact with the bared fibres, the intervention of fat or fascia or dried epineurium being sufficient to diminish or prevent the excitatory effect.

#### CHAPTER IV—THE RESTING ELECTRICAL DIFFERENCE IN THE MAMMALIAN NERVE AND SPINAL CORD

The experiments which form the subject of the succeeding sections furnished us with a large number of observations as to the amount and character of the persistent electromotive difference which exists in the Mammalian nerve and spinal cord between the cross section and surface

The number alone of the experimental observations would be sufficient to warrant their introduction at this stage in a chapter devoted to their consideration only, but as in addition they seem to furnish valuable side evidence as to the relations of the spinal cord both to the cerebrum and the issuing nerves, such an exclusive study becomes a matter of necessity

It is well known that when by means of appropriate contacts the cross section is compared with the longitudinal surface of a living nerve, an electromotive difference is found to exist, of such a character that if examined galvanometrically the surface is positive to the cross section. The current associated with this difference was termed by its discoverer, DU BOIS-REYMOND, the nerve current (*nervenstrom*), and by others, HERMANN, HERING, the demarcation current, since it is presumed by them to have its seat in the zone of tissue which at once bounds and divides the region of living from that of injured and dead or dying nerve. The use of either of these terms is, we consider, objectionable in the present instance, since our object is merely to state the actual fact without involving any cause thereof, we will therefore designate the persistent electrical difference just referred to the *resting difference*.

The difference was in all cases estimated in the following manner. By means of the long compensator, described in the preceding chapter on apparatus, a known difference of electrical potential was introduced into one part of the electrode circuit of a sign opposed to that present at the electrode contacts, and the former was then adjusted until the galvanometer showed no current to be present in the circuit, the original difference between the two electrode contacts is thus given in terms of decimal fractions of the constant external source of difference of potential. As already indicated, this source was the Callaud cell, the E.M.F. of which was itself by a similar balancing method in terms of a carefully prepared Daniell cell.



The special structures investigated fall into three classes—

- A Sciatic nerve
- B Posterior root
- C Anterior root.
- D Spinal cord

## A SCIATIC NERVE

### 1 *Amount of Difference*

The resting difference between the cross section and the longitudinal surface of the Mammalian nerve was estimated by DU BOIS-REYMOND as 026 D in the case of the Rabbit,\* a much less marked difference, 005 D, was observed by ISRAEL† in the sciatic of the same animal. The amount of the difference in the sciatic nerve was observed in various Mammals by FREDERICQ,‡ who obtained the following results —

Cat	.	017 to 018 Daniell
Dog		018 „ 024 „
Rabbit		015 „ 028 „
Duck		024 „ 026 „
Horse		004 „ 007 „

Our own results were obtained with the Cat and Monkey. In all cases the sciatic nerve of the anæsthetised animal was exposed in the popliteal space, ligatured, and divided below the ligature.

The results obtained with 69 sciatic nerves in the Cat are given in Appendix B, I, these are separated into those in which the cord, and thus the nerve, was connected with the brain, and those in which the cord was divided. The average result of both sets is the same, being 0094 Daniell in both. The influence of complete section of the nerve at the sciatic notch was also observed in some cases, and was found not to affect the amount of the difference for the first minute or two. The highest difference ever observed was Cat (70)§ and Cat (75), when it amounted to 018 Daniell, the lowest was 004. Whilst then the average amount is much lower than that which previous observers above referred to obtained in the Rabbit, the maximum corresponds to that noted by FREDERICQ in the Cat.

The results obtained in the case of the Monkey are shown in Appendix B, I. Twelve

\* 'Gesammelte Abhandl.,' vol 2, p. 250

† ISRAEL, 'Archiv f Anat u Physiol,' 1877 ('Physiol Abth,') p 451

‡ FREDERICQ, 'Archiv f Anat u Physiol,' 1880 ('Physiol Abth,') p 65

§ In all cases where a number in brackets follows the mention of an animal, *e g*, Cat (70), it refers to the page in our note ledger. The number of observations is so large that, for purposes of control and correction, we have been compelled to thus check the record.



nerves were examined and the average difference amounted to only 005 Daniell, whilst the highest difference observed was 007, and the lowest 003. This diminution in the case of the Monkey cannot be attributed to the smaller size of the sciatic nerve in the common Macaque Monkey, which is generally experimented upon, since in two cases large Rhesus Monkeys with big nerves were used, and in these (333), (368) the highest difference is 007, and the average 0055. (Compare the proportions of the nerves as shown in Plates 30-35.)

Moreover, as the previous results obtained by FREDERICQ show, the amount of the difference does not vary directly with the size of the nerve when different classes of animals are used, of which the high difference in the Rabbit and the low difference in the Horse is a notable illustration.

It will be seen that the spinal cord resting difference in the Cat and Monkey exhibits the same contrast as that of the sciatic nerves.

It has been stated that the resting difference in the nerve is not perceptibly affected by division of the spinal cord, when the division is carried out at the time of the observation. It appears, however, that section of the cord one to two months prior to the experiment does affect the amount of the difference. This influence, though small, seems to be sufficient to enable the observer to judge, when the cord lesion has been unilateral, upon which side it is situated.

Thus in an animal, Cat (227), in which the left lumbar posterior roots had been divided, the left nerve difference was 007, that of the right 009. In another animal, Cat (223), in which the right posterior column had been divided, the right nerve difference amounted to 005, the left 008, and in an animal (259) upon which a hemisection on the left side had been effected, the left nerve difference was 007, the right 008.

In one case after section of both posterior columns (Cat) the difference in each nerve was 012, an amount which is somewhat in excess of the average.

## 2. *Alterations in the Resting Difference.*

The alterations in the difference occurring whilst the nerve was under observation may be divided into .—

(a.) Those due to physical changes, affecting the contacts and derivation currents, and due to loss of moisture from evaporation, change of temperature, &c.

(b.) Those only to be accounted for as connected with slow physiological changes in the tissue, the chief agent in such alteration being loss of vitality, due to arrest of the circulation, and to other causes.

(c.) Those directly connected with the production in the tissue of excitatory physiological processes.

We will now examine these separately in detail.

(a) *Physical Changes*—With regard to the effect of physical changes, such as

temperature, drying, &c, these influence the electrical resistance of the tissue surrounding by altering the moisture with which it is infiltrated. The result is to cause an alteration in the balance previously existing between the currents due to the tissue and the compensator source. The character of this will be made evident by citing a case.

The sciatic nerve, prepared as above, and hanging free in air, was connected by its cross section and surface with the galvanometer electrodes, the resting difference between the contacts was compensated at first by a difference of .01 D. The nerve was then moistened between the contacts, this necessitating a reduction of the compensation to 0.085 D. This alteration is obviously due to the fact that the increased moisture has decreased the resistance in the surface of the nerve, and thereby increased the intensity of all currents which are present in that region. These currents are, first, a portion of the balancing current, and secondly, the derivation currents between the surface and cross section of the nerve. Whilst these two are equally affected between the points of contact of the electrodes, the result as regards the galvanometer circuit is very different. This will be rendered clear if we remember that the tissue difference is usually that obtained by connecting two surface points of a series of closed circuits, through which currents flow, and that the resistance of the circuits varies inversely with the amount of tissue moisture, so that the amount of spread, and thus the particular derivation on the surface, is diminished by the increased moisture. The final result is that, as regards the galvanometer circuit, there is now a current in the direction opposed to that due to the tissue difference, this being due to the over compensation, and rendered more distinct by the lessened resistance in the whole galvanometric circuit which the moistening involves.

The effect of drying must be the reverse of that indicated. It became noticeable in our prolonged experiments upon the Mammalian nerve and spinal cord, since it was essential for our purpose to perform the experiments in a room at about 70° F. As far as possible the errors due to this were obviated by the use of steaming sponges placed under the structures, but a slow steady rise in the amount of the difference during the first 5 or 10 minutes after the electrodes have been applied, and maintained unaltered, is usually seen in the cord, *vide infra*, and although not a very noticeable feature in nerve, may, when present, be partly attributed to this cause.

As just indicated the temperature was kept tolerably constant, but, as HERMANN and others have shown, the gradual rise in the temperature of the experimental room, may cause a similar slow increase in the amount of the difference. This alteration is, however, strictly of physiological origin, being related to a change in the molecular condition which lies at the foundation of the difference.

This brings us at once to the alterations which may be more especially ascribed to physiological changes.

(b.) *Slow Physiological Changes not Obviously Excitatory*.—The alterations of this kind in the resting difference due to physiological changes are in the case of nerve

usually a fall in the amount. Sometimes it has happened that a rapid rise for the first few minutes has been observed which did not admit of explanation as being caused by either of the two agents just indicated, and the presence of such a rise to a very marked degree in the case of the spinal cord as well as its presence in the isolated nerves and muscles of the Frog, renders it probable that in the Mammalian nerve, when present, its origin is physiological.

The fall is undoubtedly connected with loss of vitality, and may vary between the slow diminution which follows arrest of the circulation, and the rapid fall produced by injury of the nerve in immediate proximity to the surface contact.

The alterations which especially call for remark here are those which are entailed by the death of the animal on the one hand, and by the severance of the nerve from the spinal cord on the other. The first is probably due to several factors whilst the second is due both to arrest of the local circulation and the destruction of the continuity of the nerve fibres with their trophic centres in the cord.

In the case of the sciatic nerve, the alteration seemed to us to be the same in extent whichever event occurred, that is to say, the resting difference for the first 30 minutes slowly diminished in amount at the average rate of  $\frac{1}{10000}$  Daniell per minute, this rate of diminution becoming less afterwards.

It is, however, questionable to what extent in the suspended and isolated nerve, the physiological conditions which are dependent upon continuity with the cord are maintained by any facilities which the preservation of vessels affords for keeping up a circulation in the nerve, since this must be, undoubtedly, greatly impaired by the exposure. The conditions of vitality would rather seem to be linked with the maintenance of physiological connection with other nerve structures, around which an active circulation is still being carried on, and which, therefore, retain their normal vital characteristics. That this is probable is shown by the fact that when, as sometimes occurs, the nerve difference, owing to rapid drying, shows a steady rise in amount, which rise continues even when no evidence of circulation in the exposed nerve is obvious, the rise is immediately counterbalanced and converted into a fall on systemic death of the animal, this fall occurring *pari passu* with the loss of excitability in the central nerve structures.

(c.) *Physiological Changes Connected with Excitation* —The alterations due to excitation were after effects, that is, they followed the development of the transient excitatory change and consisted in a permanent slight diminution in the previously existing difference, such as has been observed to follow nerve excitation in the case of the Frog.

The slow after effect can be readily distinguished from the transient rapid electrical changes due to the actual presence of excitatory processes evoked by the application of the stimulus, since these are synchronous with the excitation, whereas the after-effect is very variable in its duration, but always follows cessation of the stimulus, and persists for many seconds.

We have noticed that it is more pronounced when the etherisation has become slight in degree

In addition to the after-effect due to excitation there are seen under certain circumstances, particularly that of inadequate etherisation, changes in the nerve difference, which in the galvanometer indicate their presence by the needle now slowly rising 30 to 50 scale, and now falling. These disappear when the anæsthesia is rendered more profound, and are much more marked in the case of the spinal cord, they are probably due to the occasional discharge of groups of minimal nerve impulses, and are analogous to those first observed in the medulla of the Frog by SETSCHENOW.

## B. POSTERIOR ROOT

### 1 *Amount of Difference*

We have made six experiments upon the posterior root. In these a lumbar posterior root was exposed, ligatured, and divided as close to the ganglion as possible, without involving this structure, and the root thus left connected with the cord was suspended in air by the attached thread. The particular root chosen in five cases was the 7th of the lumbar series, since this is the largest in the Cat of the roots forming the lumbar plexus (see Plate 35). The galvanometer electrodes were attached, as in the nerve, by means of thread cables moistened with 6 per cent NaCl, to the cross section and the longitudinal surface, and the amount of the resting difference determined by the balancing method.

The result in the five animals was found to be 0.26, 0.2, 0.2, 0.18, and 0.16 Daniell respectively.

Hence although the 7th lumbar root is less than half the size of the sciatic nerve, the average amount of the resting difference, 0.2, is about twice as large. (The 6th lumbar root was observed once, the difference being 0.12.) This remarkable circumstance is very significant when the proximity of the structure to the spinal cord is taken into consideration, and deserves a more extended investigation. It may be pointed out that SCHIFF observed that there was a resting difference between contacts when placed upon a more central and a more distal portion of a continuous nerve, the central contact being positive to the other, also that excitation of any portion of the tract caused an excitatory change, in which the tissue under the first contact became galvanometrically negative to that under the second more remote one.

Further, both GRUNHAGEN and BERNSTEIN have noticed that the central portions of the nerve are more excitable than the distal portions. Now whether the persistent difference be fundamentally the same in kind as the transient excitatory electrical change or not, there is an undoubted quantitative relationship subsisting between the two. It is, therefore, not surprising that there should be found an increase in the amount of the resting difference obtainable in the posterior roots as compared with the sciatic nerve.

2 *Alterations in Resting Difference*

(a) *Physical Changes*—The alterations due to drying probably have the same influence as that already alluded to in the case of the sciatic nerve. The amount of the difference noticed immediately after section generally increases slowly and steadily, and, at least partially, from this cause. There is, however, a noticeable check in the rise after the first five minutes, after which the difference then only in some cases begins to fall. Hence either the rise is accentuated at first by some other agency, or it is counterbalanced by the depressant effects due to loss of vitality.

(b.) *Physiological Changes*—The amount of the difference in the root diminishes with greater rapidity than in the case of the nerve trunk, in consequence of systemic death. A similar fall occurs if the root is severed from its central connection. This is illustrated by the following series of experimental observations made before and after the death of the animal.

## LEFT 7th Lumbar Posterior Root \* (Cat, 362.)

Root Divided near Ganglion and Central End Connected with Electrodes

	Time of observation	Amount of difference
Excitation experiments carried out .	11 42	019
	11 45	02
	11 51	0195
	11 55	019
	12 0	
Systemic death	12 3	0185
	12 12	018

## Root cut off from Cord.

Time of observation	Amount of difference
12.13	0175
12 14	017
12 15	016
12 16	0155
12.18	015

In another animal after systemic death had caused a decline in the amount of ice, severance of the root caused no further appreciable decline.

\* See Plate 35

The root, therefore, in this respect behaves, as far as these two experiments enable us to judge, like the nerve

(c.) *Changes following Excitation* —In consequence of either direct excitation of the root or its indirect excitation through the cord, the amount of the difference is decreased, an after-effect following the passing away of the true excitatory change similar in character to that seen in the nerve

The rising and falling in the amount of the difference when the anæsthesia of the animal is not sufficiently profound is rather more marked in the case of the posterior root than in that of the mixed nerve.

### C ANTERIOR ROOT

With regard to the anterior roots, we have only performed one experiment. There are considerable difficulties in the way of connecting the anterior root satisfactorily with the electrodes, so as to exclude all possibility of obtaining results which are derived from electrical changes in the cord. These difficulties are mainly the shortness of the root and the characters of its anatomical relations with the cord, it being difficult to obtain a sufficient length. Moreover, our purpose being rather to obtain the evidence of excitatory than of resting electrical changes, the shortness of the root, when combined with the movements of the animal, caused serious errors in observation, due to the displacement of the electrodes and their being thus brought near to or in contact with surrounding structures. In the single case in which the 6th left lumbar anterior root was divided and its central end connected with the galvanometer electrodes, the difference (Cat) was found to be only 0.045 Daniell, whereas the 6th lumbar posterior root of the same side, when examined, showed a difference of 0.12 Daniell.

### D SPINAL CORD

The fact that the cord exhibits, like the nerve, both a persistent difference between its longitudinal surface and its cross section and a true excitatory effect, was discovered by DU BOIS-REYMOND, and has been since confirmed by other observers, notably SETSCHENOW. The general features of the same were described by us in our preliminary communication made to the Royal Society, but a systematic analysis of a number of observations has never, that we are aware, been made, nor has the amount of the persistent difference been determined. In the course of our investigations we have noted the amount and characteristics of the resting difference in the spinal cords of sixty-three Cats and fourteen Monkeys, and the results arranged in groups are given in Appendix B.

The most striking characteristics of the resting difference in the cord and the contrast between this difference and that of the nerve may be roughly seen after the death of the animal (Cat, Rabbit, &c.) by rapidly exposing a length of cord and of



the sciatic nerve, removing the exposed portion of each, placing it on a glass plate and bringing one electrode in connection with the cross section, the other with the longitudinal surface of the preparations. It will be found that in the Cat the nerve difference amounts to little over 0.1 Daniell, whereas the cord difference amounts to 0.25 to 0.3 Daniell or more. That this contrast is not merely a question of cross sectional area is shown by experimenting with the dorsal cord of a small (young) animal and with the large nerve of a full grown adult animal of the same species, when the same relations will be found to still hold good, viz., the cord difference twice to three times the amount of that of the nerve.

For purposes of experimental investigation however, the spinal cord was exposed in the lower dorsal or lumbar region under all the precautions mentioned in the paragraph upon operative procedure, it was then divided and freed as required on either the central or peripheral side of the division for 4 or 5 centims. from all its attachments, the severed end was ligatured and this portion of cord raised from the canal and suspended in air by a ligature, still retaining its continuity with the exposed cord at its deep attachment. The raised portion was in some cases that on the central side of the section, in which case the continuity with the brain was preserved, in others that on the peripheral side, in which case the connection with the sciatic nerves was preserved.

### 1 — *Amount of Difference*

(a) *Whole Cord* — If an average of the various results obtained in the case of fifty Cats is taken, the exposed cord being normal and always in connection by its deep attachment with a portion of cord *in situ*, but without distinction of the nature of this attachment, it will be found that the average resting difference in the Cat is 0.32 Daniell, the highest difference being 0.46 Daniell, the lowest 0.14 Daniell.

A similar average of the results in nine Monkeys gives a resting difference of 0.22 Daniell, the highest difference observed being 0.29, the lowest 0.13.

It is thus evident that the relationship between the amounts of the resting difference obtainable in the Cat and Monkey holds good for both the sciatic nerve and the cord, the amount in the Cat being very appreciably larger than that in the Monkey. The notable increase in the size of the resting current in the cord as compared with the nerve of the same species will be rendered evident if we place side by side the average results of the two. Thus. —

$$\frac{\text{Cat cord}}{\text{Cat nerve}} = \frac{0.32}{0.095} = \frac{3.3}{1}.$$

$$\frac{\text{Monkey cord}}{\text{Monkey nerve}} = \frac{0.22}{0.05} = \frac{4.4}{1}.$$

this increase in the proportion of about 4 to 1 is not merely due to increased



size has been roughly indicated previously, this will, however, be more clearly exhibited by the consideration of the ratio which a similar comparison between the difference in the cord and in the posterior root of the Cat shows —

$$\frac{\text{Average Cat cord}}{\text{Average Cat posterior root}} = \frac{032}{\cdot 022} = \frac{1.5}{1}$$

It is probable therefore that the larger difference is in some way correlated with the structure of the cord and the trophic and other physiological influences which that structure implies

This explanation is supported by an analysis of the results obtained in the two species of animals when the cord is placed under different conditions as regards its central connections. Such analysis involves the grouping together on the one hand of all those determinations in which the cord was still in connection with the cerebrum and its central end investigated, and on the other hand of all those in which the portion of cord examined was that of the lower fragment unconnected with the cerebrum

The first group shown in Appendix B, III, gives the average result in the case of the lower dorsal cord of fourteen Cats, this average being 034 Daniell, the highest amount observed being 046, the lowest 025

It also gives the average result in the case of five Monkeys, this being 025 Daniell; the highest reading being 029, the lowest 018

If now, we turn to the second group, the average in the Cat of all the readings in the dorsal and lumbar regions respectively when the Cat's cord is severed from the brain, amounts to —

Dorsal region, 24 cases, average	029
Lumbar „ 10 „ „	033
<hr/>	
34 cases	

Gross average = 03 Daniell

Highest = 043; lowest = 014

In the Monkey a similar average of four sets of experiments gives 019 Daniell, highest 027, lowest 013

A comparison of the two groups of results may now be made as follows —

Cat—	
Cord connected with brain	034
Cord severed from brain	03
Monkey—	
Cord connected with brain	025
Cord severed from brain	019

The comparison shows that the amount of the resting difference in the anæsthetised animal is larger when the cerebral connections are intact

This conclusion is supported by direct experimentation upon the influence of severance. Thus in an anæsthetised animal (Cat) the cord was exposed and divided at the level of the 4th lumbar vertebra and the central end ligatured. It was then suspended in the usual way and the electrodes attached to the cross section and the longitudinal surface. The resting difference amounted to 0.44 Daniell, whereas, when the cord was severed higher up at the 7th dorsal vertebra, a notable fall to 0.37 Daniell occurred.

In another experiment (Cat, 315) the cord was divided at the 13th dorsal vertebra and similarly prepared. Its central end was then connected with the galvanometer electrodes as above. The amount of the difference between the surface on the central side of the cross section and the cross section itself amounted to 0.4 Daniell. A hemisection of the cord at the 8th dorsal vertebra was now made and the difference fell rapidly to 0.38 Daniell, the rapid fall then ceased, but a slow fall continued for some time.

These experiments suggest that severance in an anæsthetised animal of the cord from the brain causes a direct diminution in the amount of the resting difference below the point of severance, whether by the interference with the circulation which such severance may imply, or by this aided by the interruption in the path which joins at any rate some of the (pyramidal) fibres with the cells with which they are in direct connection and which govern their nutrition. As will be seen later there is no evidence of a similar diminution being produced when the cross sections are made upon a portion of cord already severed from the brain by an interruption higher up. Hence the inference that the fall is correlated with the interruption (in the pyramidal fibres?) is strengthened.

Finally the region of cord investigated has some relation with the amount of the resting difference. This is shown in Appendix B, III, in which observations made in the dorsal region are separated from those in the lumbar region.

The average of the dorsal region = 0.29; highest 0.43, lowest 0.14

The average of the lumbar region = 0.33, highest 0.4, lowest 0.28

Although the average seems to show that the difference in the dorsal cord is less than that in the lumbar, yet an examination of the highest and lowest limits suggests that the preponderance, in the latter case, is due to the fact that in the dorsal cord several very low readings were obtained. (See Table (2); Appendix B, III., Cats 194, 289, 349)

We have endeavoured to get some notion of the relations of the different regions by exposing in an anæsthetised animal (Cat 36) the whole cord. This was then divided into three equal lengths, comprising the cervical, dorsal, and lumbar regions respectively, and the three placed in a warm moist chamber for examination.

The examination was made as rapidly as possible in the order given below, and at the various regions indicated

Lumbar segment—

From 4th lumbar                      ·035              to about 11th dorsal              04.

Dorsal segment—

From about 11th dorsal              043              to about 3rd dorsal              037.

Cervical segment—

From about 3rd dorsal              035              to about 3rd cervical              037

After a quarter of an hour's interval, the experiment was repeated in the reverse order, commencing with the cervical and ending with the lumbar segment. The results were as follows —

Lumbar segment	.	035	·036,
Dorsal segment		·030	021,
Cervical segment		·031	029

In this experiment, the dorsal cord resting difference is greater than that obtained from either enlargement, but it is more affected by the injurious influences of severance and loss of circulation. It must be remembered, that there are three possible factors in the severed cord which determine the amount of the resting difference in any given region, the number of fibres, the amount of grey matter, and the maintenance of vitality through circulation, &c, this last being influenced by size of vessels, &c. All these vary in different regions, but the first is preponderant in the dorsal region, the others in the enlargements.

(b.) *Cord Divided Longitudinally*.—In the course of experiments to be detailed hereafter, we had occasion several times to divide the cord longitudinally into two halves. This division was carried out under all the precautions indicated in the section dealing with operative procedure, and was always in the form of a longitudinal cut connecting the anterior and posterior fissures, and extended from the cross section of the divided cord for three centimetres. Since it was our main object to establish a quantitative comparison between the crossed and the direct excitatory cord effect evoked by cortical stimulation, the cord was generally divided in the lower dorsal region, and the lower end of the fragment on the central side of the division was split in the fashion just described. (See Plates 31, 33) The results in seven Cats and five Monkeys are given in Appendix B, III.

Each half of the split cord was connected with a pair of non-polarisable electrodes by the cable arrangement already indicated, and the amount of the difference between the cross section and the surface in each then determined. It will be seen that the average amount for each side in the Cat is ·02 Daniell, the highest and lowest readings

being .029 and .01 in the case of the left side, and .027 and .014 in that of the right side.

In the Monkey, the average result for the left side is .016, that for the right .011. It will be noticed that in each animal the sum of the two readings is slightly larger than the average for the unsplit cord.

A further table (4) gives the results of a similar splitting operation carried out on the upper end of the lower peripheral fragment of the divided cord in two Cats.

In one Cat (137) the left half of the split cord showed a resting difference of .007, and the right .016, in the other Cat (143) the left half showed .021, and the right .013. The amounts are considerably below those just mentioned, one reason doubtless being the fact that the portion of cord upon which the operation was carried out was severed from the brain.

(c) *Cord previously operated upon.*—It has already been pointed out that, while severance from the brain seems to induce a condition in the separated cord in which the amount of the resting difference is less than it otherwise would have been, further operations upon this severed fragment do not seem to notably affect the difference, provided they are made in such situations as to leave a part of the cord both intact and *in situ* between their seat and the portion observed.

That is to say, the difference in the lower fragment of a cord severed from the brain is not further diminished by exposing it again in its continuity and performing there either section of one or of several columns.

It is different, however, when such operative lesions have been performed several weeks before the experimental investigation. In these cases the average amount of the resting difference observed was .022 Daniell, that is less than the normal, but the differences between the experiments are best shown by reference to the column in Appendix B., III (5). They will then be found to vary between .012 (cord one month after section of posterior roots), and .038 (cord four months after hemisection on left side). This last is an exceptionally high result when compared with that obtained after a very similar two months' previous hemisection when the amount of the difference was only .017, and also that obtained after a one month's previous hemisection on the opposite side, when the amount was .018.

In a case of one month's previous lesion of both posterior columns, the amount of the resting difference was found to be .022, and after a lesion of one posterior column it was found to be .025.

If .030 is taken as the average amount of the difference in the normal Cat, after severance of the cord from the brain, then a descending series occurs in these cases, as shown in the table, in all of which with one exception the demarcation current is below the normal, and the average of these, when this exceptionally high and contradictory result is excluded, would be .019 Daniell.

## TABLE of Results after Previous Operations.

·012	after section of posterior roots.
017	„ hemisection.
018	„ „
·022	„ section of both posterior columns.
·025	„ „ one „ „
Total ..	094
Average..	019 Daniell approx.

2. *Alterations in Resting Difference*

The electrical difference between the surface and cross section of the spinal cord alters during observation in the manner already described in treating of the sciatic nerve and root, but the alterations are much more marked

(a.) *Physical Changes*.—The effect of drying is the same as in the case of the nerve, the amount of the resting difference continuing to rise steadily after exposure and isolation of the cord unless great care is taken to keep it moist. It is difficult to ascertain with precision to what degree this physical change is capable of causing a rise in the difference, this rise being about 0001 Daniell in five minutes, but that it is by no means the sole agent is shown by the fact that even when the exposed cord is kept moist by steaming sponges with as much care as possible, the rise continues, though more slowly than when no such precautions are used, as also by the facts to be referred to in the succeeding paragraphs. It is, however, important to keep in view in the consideration of alterations supposed to be due to strictly physiological agencies the influence of these purely physical ones

(b) *Physiological Changes not obviously Excitatory*.—The alterations due to physiological changes are associated with both a rise and a fall in the amount of difference, and are much more marked in the case of the cord than in that of the nerve or the root. The amount of the rise is demonstrated in the following observations, in all of which the cord having been exposed, ligatured, and divided, was suspended by its unattached end and connected with the electrodes in the manner described before.

It was then observed that in every case the resting difference between the surface and cross section increased rapidly for the first five minutes or more after the isolation had been made, provided that the cord was still in connection by its deep attachment with a part which, being *in situ*, was in its normal physiological state of nutrition. The amount of this initial rise varies considerably in different cords, but the average in 19 cases amounted to ·0016 Daniell, the highest rise being 003 and the lowest 001. The duration of this comparatively rapid rise is, on the average, about five

minutes This initial increase is probably of the same character as that observed by DU BOIS-REYMOND, HERMANN, ENGELMANN, and others in both muscle and nerve, and is in some way related to the development of changes produced by the cross section

The difference continues very slowly to increase in the unstimulated cord, at a rate of about 0001 in five minutes, this change being probably connected with interstitial drying There is, however, a marked increase in the difference when the cord is aroused by successive stimulation, and this last rise is the most striking and novel feature displayed by the cord it will be treated of under the excitatory changes

If systemic death occurs, the difference immediately begins to decline, and this is such an invariable result that we have often observed the first approach of death by the behaviour of the galvanometer needle On separation of the cord from the body a similar decline occurs, the rapidity of which is shown by the following results —

#### DECLINE in Difference following Systemic Death

		5 minutes	10 minutes	15 minutes	20 minutes	25 minutes	30 minutes
Cat (246)	029	028	026	024	023	022	
Cat (258)	031	03	028	026	025	024	023
Cat (323)	039	038		.	.	.	03
Cat (345)	04	037					

From the above cases it will be seen that on systemic death the resting difference declines to such an extent that in half an hour the total fall amounted to .007, .008, and .009 Daniell How far this fall is associated with the cessation of the circulation in the actual portion of exposed cord under investigation is a moot point, but the reasons brought forward on p 283 with reference to the similar question in the case of the sciatic nerve are applicable to that of the spinal cord The local circulation is undoubtedly seriously impaired by the exposure; it is, therefore, rather to the structural connection with the portion of cord *in situ*, in which the circulation is adequately maintained, than to the integrity of its own blood supply that the maintenance of the difference in the case of the living animal must be ascribed. It is wonderful what prolonged exposure a portion of the spinal cord will sustain without losing its excitability, provided only that the local conditions of adequate moisture and warmth are fulfilled and that a structural connection is kept up with normal unexposed cord substance.

The above decline is contemporaneous with a marked lessening of excitability As is shown in the chapter upon cord excitation, all evidence of excitatory change in response to stimulation disappears a few minutes after systemic death.

If the fragment of exposed cord is wholly removed from the animal, the difference

rapidly subsides, as is shown in the experiment described on p 313, as made upon such pieces of spinal cord

The decline in the difference thus produced, seems to occur with greater rapidity than in the case of systemic death. It is illustrated by the following experiment upon the cord of the Cat (354), in which, at the close of an exposure and series of investigations, which had lasted an hour and a half, the exposed piece of cord was cut free from its deep attachments, and the consequent decline in the resting difference noted

This difference had previously been rising all through the experiment, ever since the cord which had been exposed and divided at the 1st lumbar vertebra was first examined. The portion investigated galvanometrically was on the central side of the above section, but the upper part of the cord was not connected with the brain, since a second complete section at the level of the 7th dorsal vertebra had been made for purposes of stimulation

The amount of the initial resting difference between the cross-section and surface of the investigated portion observed (at 11.4) was 0.33 Daniell, at the close of the experiments (12.39) it was 0.38; the exposed portion of cord was then severed from its deep attachment so as to be wholly detached, in two minutes (12.39) it was 0.37,

(12.41)	.	.	0.36
(12.43)	.	.	0.34
(12.45)	.	.	0.33
(12.47)	.	.	0.32

That is to say, a fall in the difference amounting to 0.06 occurred in ten minutes, in another hour the difference had fallen to half its original amount = 0.19 Daniell

Both the slower fall in consequence of systemic death and the more rapid fall in consequence of a complete detachment from the rest of the nervous system, contrast with that produced by the change following injury sustained by the cord even when *in situ*. The mechanical injury which seems most fatal to excitability, is that produced by stretching of the cord, a sudden pull being followed almost immediately by the disappearance of any excitatory effect and by a rapid fall in the resting difference. Thus, in one animal (Cat 126), the difference was 0.35, but owing to the arrangement for fixing the spine, &c, becoming loose, the suspended cord was pulled by a movement of the preparation, and the difference fell suddenly to 0.17. The whole cord, however, was not injured, but only the portion observed, for a new dissection exposed a fresh part and a higher section was then made, which gave a difference of 0.28

(c) *Physiological Changes connected with Excitation* —It has been already indicated that a characteristic feature of the spinal cord difference is the alteration produced in it by stimulation. It will be seen by the experimental details, which are set forth in the following chapters, that marked excitatory electrical effects are evoked



in the cord by stimulating either the cortex of the brain, the different regions of the cord itself, or the issuing posterior roots. These effects resemble in character those evoked in the nerve trunks themselves, the electrical change commences with the stimulation, is opposed in direction to the resting difference, and subsides on the cessation of the stimulus. Following this true excitatory effect is an after-effect, which is characterised by an increase in the previous difference.

In any given experiment the after-effect shows itself thus. The cord having been exposed, divided, prepared, and connected in the usual way with the electrodes by its cross section and its longitudinal surface, the amount of the resting difference was noted. This difference rises as just stated for the first few minutes, and then remains very nearly steady. The cord is now excited in any of the three ways mentioned above; an electrical change occurs, *i.e.*, a current opposed to the difference is present in the galvanometer circuit which, on the cessation of the stimulation, subsides. The galvanometer needle, which evidences the existence of this current, having moved from its resting zero position through a certain deflection, returns to its previous position. If the nerve were the tissue under investigation, this return would be not quite complete, but with the spinal cord it is characterised by continuing beyond the zero position to a point considerably the other side, after which the needle slowly moves back again towards zero, which, however, it does not reach. As the result of excitation, therefore, the previously balanced difference is no longer compensated, a current persists in the circuit in the direction of that produced by the difference, and to compensate this, and thus bring the needle back to zero, the balancing circuit has to be readjusted.

In short, the excitation has caused, after the usual negative variation, a permanent rise in the resting difference between the two electrode contacts. This, positive after effect is not unknown in other structures, it occurs occasionally in both muscle and nerve preparations of the Frog (HERING, HEAD), but the conditions necessary for its production are but imperfectly ascertained. It is, however, as far as we know, invariably present in the case of the spinal cord of the Cat and Monkey, though its amount is very variable in different preparations.

In almost all cases the amount of the rise is dependent rather upon the condition of the preparation than either the intensity or duration of the cord stimulation. It is greatest as a consequence of the earlier stimulations, and becomes less and less with a repetition of the stimulus.

If, therefore, a series of experiments are made involving the stimulation of the cord at successive intervals, the resting difference rises at first rapidly, and then more slowly, until after 20 to 30 stimulations in from 30 to 45 minutes, the rise finally practically ceases.

The stimulus used, whether applied to the cord or to structures connected with the cord, was in all cases that of the alternating induced current previously alluded to in the chapter on the experimental method. The amount of the total rise observed in

different cases varied according to the seat of the stimulus which evoked the cord change. This seat may be either (A) *Brain*, (B) *Nerve*, or (C) *Cord*, and the cases in which we specially noted this change are as follows —

A. CORTICAL Excitation    Cord connected with Cortex.

	Initial difference	Final difference	Total rise
Cat (114)	037	039	002
„ (124)	046	047	003
„ (126)	036	040	004
„ (308)	033	036	003
„ (319)	030	035	005
„ (323)	032	033	001
Monkey (234)	026	029	003
Average rise			003

B NERVE Excitation (sciatic)    Cord severed from Cortex

	Initial difference	Final difference	Total rise
Cat (121)	031	034	003
„ (143)	032	035	003
„ (145)	028	035	007
„ (148)	023	026	003
„ (153)	025	029	004
„ (192)	023	030	007
„ (194)	017	020	003
„ (327)	023	034	011
„ (339)	022	030	008
„ (344)	022	025	003
„ (170)	026	029	003
Average rise			005

## C CORD Excitation Cord severed from Cortex.

	Initial difference	Final difference	Total rise
Cat (196)	017	030	013
" (244)	027	029	002
" (245)	021	026	005
" (357)	032	038	006
" (366)	030	037	007
" (355)	037	041	004
" (371)	028	035	007
" (375)	032	045	013
" (378)	027	029	002
" (243)	027	029	001
" (354)	033	038	005
Average rise			006

These results indicate (1) that the rise in the difference is occasioned not merely by the direct application of the stimulating agent to the cord, but as a consequence of the presence of a series of excitatory processes, whether these are produced by nerve impulses entering below by afferent channels, or from above by cortical efferent ones. This conclusion is supported by the fact that a similar rise follows a large reflex discharge of energy from the cord, when this is produced in the strychnised animal by sensory stimulation.

(2) They also show that the rise is least in the case of the excitatory cord changes evoked by cortical stimulation, in which case the limit of rise is not only small, but soon attained, the average rise in the instances given under A being  $\cdot 003$ , the maximum =  $005$ , the minimum =  $\cdot 001$ . When the sciatic nerve or posterior root of the cord (severed from the brain) is excited, the rise is seen to be much more pronounced, being on the average  $005$ , maximum  $\cdot 011$ , minimum  $\cdot 003$ . Finally, when the columns of the cord itself are excited, the rise is greater, the average being  $\cdot 006$ , maximum  $013$ , minimum  $002$  (The average rise in this case would be still greater if the three very low and exceptional readings of  $002$  were omitted from the table; it would then be  $0075$ .) In the same experiment performed on the Monkey (232) the rise in half an hour following twelve excitations was  $\cdot 006$

It would thus appear that one of the main features in the rise is the extent to which the nerve structures in the cord are thrown into activity, the result of cortical excitation is to awaken impulses in a more limited area of the cord than is the case with excitation of the sciatic afferent nerve fibres, and this latter does not cause such a widespread awakening as is produced by direct cord stimulation

From these results alone no conclusions of a definite kind can be drawn as to the relations subsisting between the cord and the brain on the one hand, and the cord and the nerves on the other, but if the amount of resting difference may be truly

taken to be an indication of the amount of potential energy, which the nerve material is capable of making kinetic in the form of a nerve impulse, then this remarkable rise, and the conditions which determine it, would appear to show that the physiological characters of the structure upon which the storage of energy depends, are such as to be rendered more efficacious with use, and that the central structures (cells) of the cord play the most prominent part in this influence of functional use upon efficiency.

#### CHAPTER V—ON THE ELECTRICAL EFFECTS EVOKED IN THE SPINAL CORD AND MIXED NERVES BY EXCITATION OF THE CORTEX CEREBRI

The primary object of this work being the determination of the nature of the impulses which issue from the excitable or so-called motor cortex, considerable importance attaches to positive results on this point. As, however, usually happens in the employment of a new method, we have found that more actual advance was made by applying it to the study of the lower centres and fibres through which these impulses pass than by attempting to elucidate the functional relations existing between one part of the cortex and the rest of the encephalon.

One fundamental fact stands out, however, prominently, *viz*, that, as we shall see directly, it is possible to ascertain and judge the nature and comparative amount of the electrical changes which accompany the descent of the cortical impulses in the spinal cord, and so to learn the character of the cortical discharge. Practically, therefore, the results of our special investigation of the excited cortex will best be arranged according to the part of the nervous system in which the electrical changes were observed. A further subdivision of such a classification will be necessary in order to bring out the wider points of interest which have received elucidation by the use of this method, and this is furnished by the summary and arrangement we have given on pp 272–276, of the facts discovered by other methods, of which the most notable are those of simple inspection and of graphic record respectively.

In accordance with this plan, therefore, we will commence with considering the case in which we observed the electrical changes in the dorsal cord, with the object of ascertaining the character of the descending nervous impulses in consequence of stimulation of the cortex.

We have employed in these experiments on the relations of the cortex cerebri to the bulbo-spinal and peripheral systems fifteen Monkeys and thirty-two Cats.

## EXCITATION OF CORTEX

1 *Electrical Changes Observed in the Spinal Cord*

The arrangement expressed in the above headings is the fundamental experiment designed to elucidate, if possible, the nature of the impulses which pass from the cortex to gain and traverse the bulbo-spinal centres. The desirability of avoiding shock, which so markedly lowers the excitability of the cortex, led us to choose to investigate the electrical effects which accompany the impulses as they pass through the mid dorsal region, so that the section of the cord was made in the Cat immediately below this point, and in the Monkey, just above or through the uppermost part of the lumbar enlargement (See figs 4 and 5.)

This selection of the seat of section had the additional advantage that it enabled us to proceed at once to the determination of further points, viz., the localisation of the upper and lower limb areas in the cortex, and thus to generally control the results obtained, as will be shown presently. We will first describe a typical experiment.

The anæsthetised animal having been arranged as described (Chapter III) the dura mater was exposed over the so-called motor area of the lower limb, the spinal cord was then exposed at the level of about the 7th dorsal vertebra, raised in air and connected to the non-polarisable electrodes. The character of the resting electrical difference between the cut end of the cord and the uninjured surfaces of the columns was noted as set forth in Chapter IV.

*(a) Effects seen in the Electrometer.*

The electrodes were, in the first instance, connected with the capillary electrometer.

The dura mater was then opened, and the surface of the cortex excited (*vide* p. 299). The effects observed in the electrometer were—

(1.) A persistent negative variation of the difference lasting as long as the excitation was applied to the cortex.

(2.) A series of intermittent negative variations commencing (sometimes after a short interval had elapsed) from the cessation of the excitation, and continuing for a variable period according to the state of the cortex.

We may with advantage at once briefly review the general questions raised by this result, as such a discussion will make clearer the object of further researches.

The effect seen in the electrometer was so identical in character with that obtained from the muscles in an epileptiform convulsion started by similar excitation of the cortex as to suggest that the essential features of the muscular convulsion are wholly due to the character of the cortical discharge. This is illustrated by the

Fig 4 \*

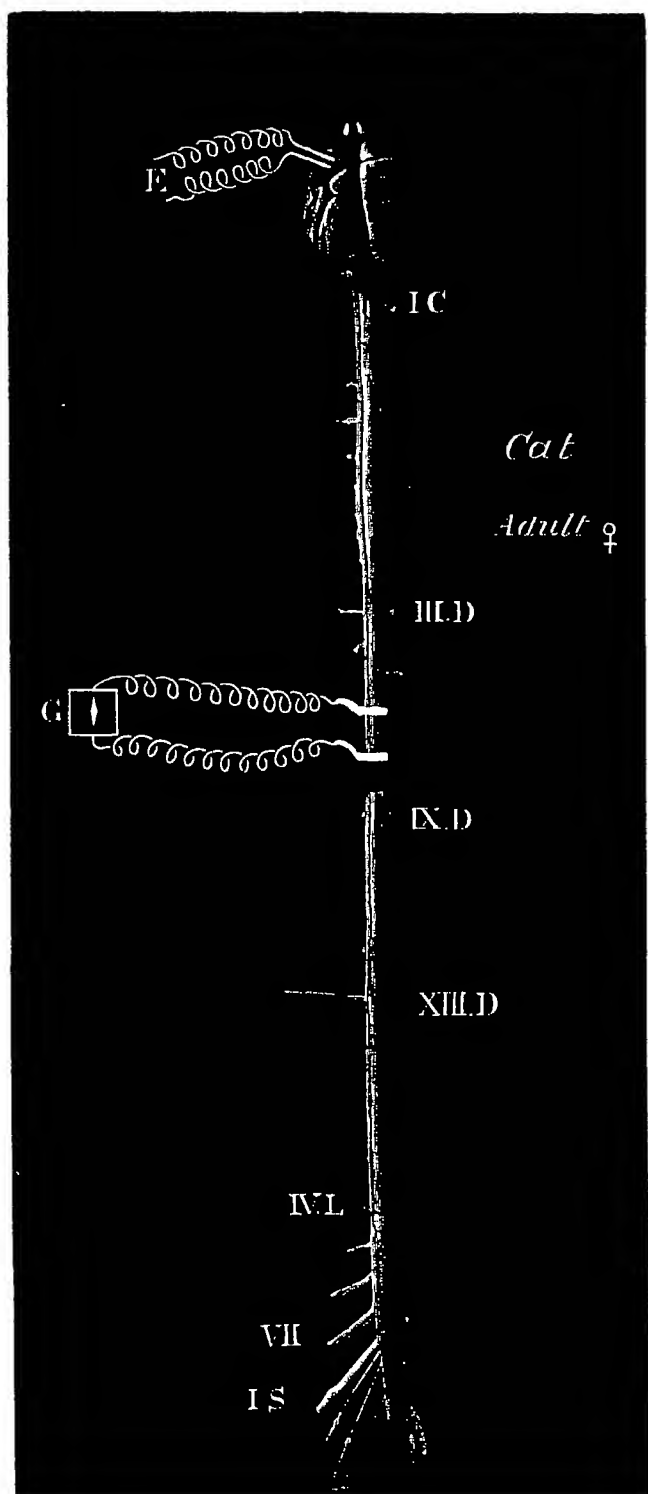
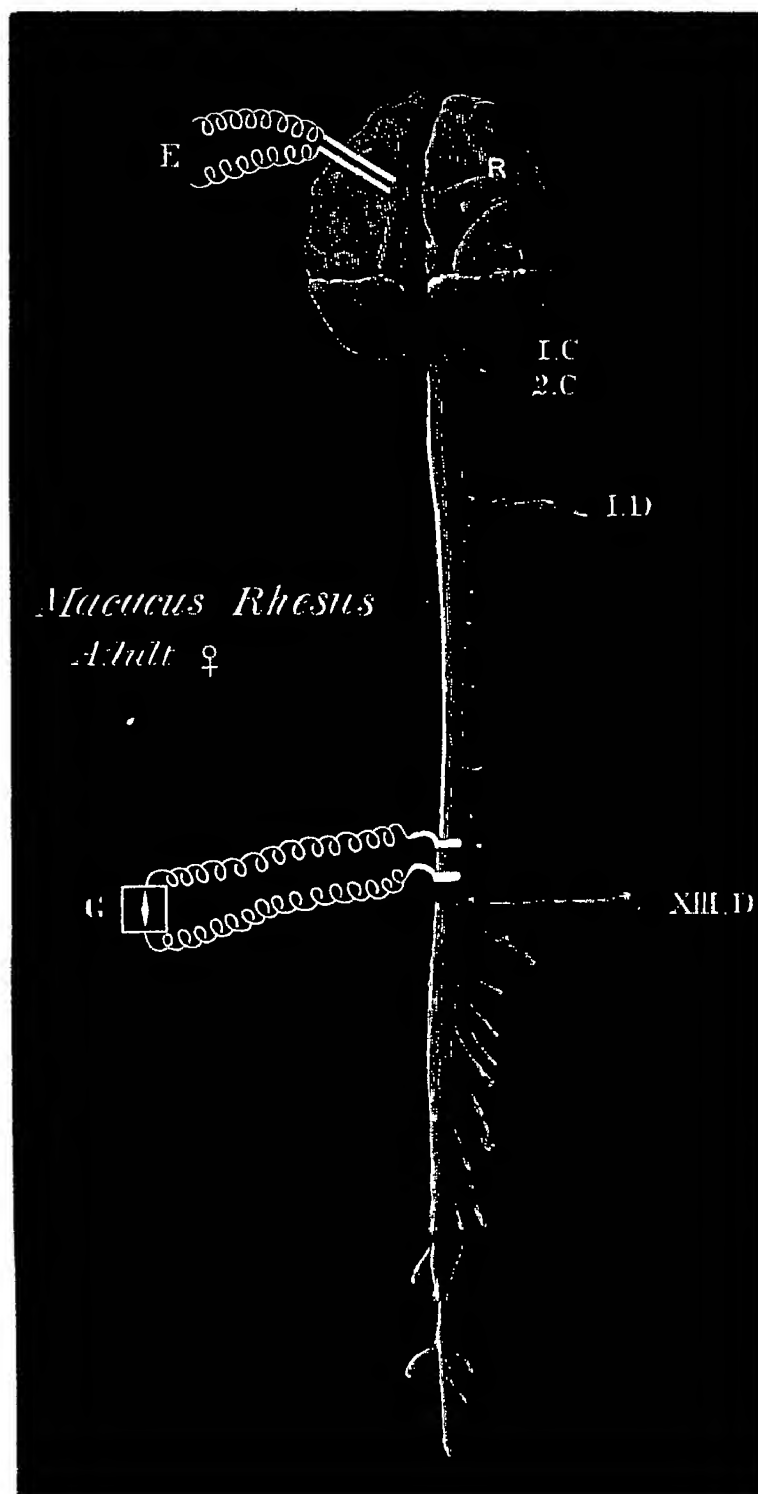


Fig 5



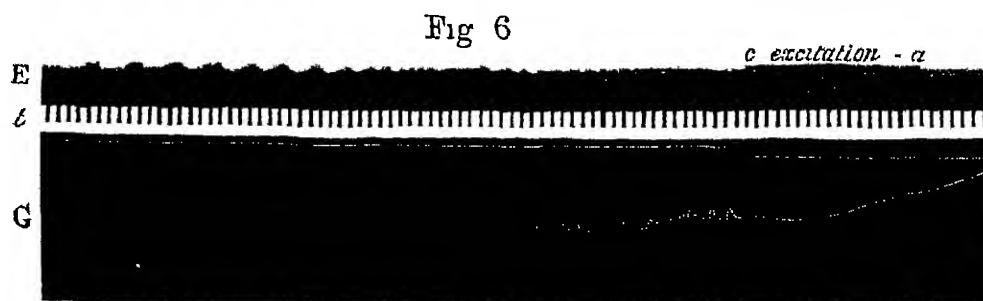
\* The central nervous system displayed in this and succeeding figures is a photographic reduction of a full size photograph of an actual dissection, as shown also in Plates 30-33. By this means, exact topography of all experimental details (i.e. position of electrodes, &c.) has been preserved. It is, perhaps, hardly necessary to add that the amount of cord exposed is shown in Plate 29.

annexed woodcut (fig 6), in which two records, one of the muscle, the other of the movement of the electrometer, are contrasted. The lower tracing, G, is that of the muscular movements of the rectus femoris of the Cat, the upper, E, is that of the movements of the projected image of the mercurial meniscus of the electrometer photographed on a sensitive plate. The juxtaposition of the records was effected by a photographic reduction of the two tracings. It is necessary to point out that exact comparison is not possible, since the two records were obtained from different animals, they are, however, comparable in this sense, that since we have selected in each case fits of about the same degree of intensity, the general fused character of the first stage, and the interrupted character of the second stage, is similar in each.

Further, the change in character of the interrupted stage itself as the fit draws to its close is very noticeable, the great increase in the extent of each clonic spasm accompanying the slower rhythm is, as will be seen, a feature common to both records.

It will now be advisable to consider in more detail the character of these electrical variations.

A reference to the photograph of the movements of the electrometer, in fig. 6, will show that the first stage of the effect produced in the cord by exciting the cortex, *i.e.*, the tonic variation lasting during the period of excitation, is a complete fusion of impulses, so that it is with our present instruments impossible to detect any waves or intermissions in it. In this respect the tonic stage exhibits no



E Photograph of movements of electrometer

G. Tracing of contracting muscle.

t Tracing of time signal with intervals of  $\frac{1}{10}$ th sec

difference from the tonus obtained by exciting the corona radiata after the cortex is removed. It is otherwise with the graphic method, see p. 273, in which a rhythm or period can be seen, showing the tonus to be an imperfect fusion of contractions. Until the question is re-examined with still more delicate instruments, it must be left entirely open, as the absence of intermittence in the electrical record may be due to instrumental inadequacy. We cannot, however, refrain from suggesting that it may be possibly a genuine phenomenon, and that the waves seen often on the tetanus curve, in the graphic method, may be in relation with blocks in the motor path; one such block we have found to be offered



by the bulbo-spinal centres to the passage of the impulses, from the spinal cord out into the nerve (see p 458, Chapter X) The further recent experiments of WEDENSKII\* seem to suggest that these waves in the muscular record may be to some extent in relation with the block offered by the motor endings of the nerves in the muscles, since he finds that such muscular intermittence may be produced by stimulation of the nerve itself with rapid rates, an intermittence which, not being synchronous with the rate of stimulation, but having its own rhythm, is presumably referable to the neuro-muscular mechanism

As regards the after effect, the clonic stage, it is frequently separated from the tonic stage by a distinct pause or interval, this is of course visible in all methods of exploration, to which the electrical investigation of the spinal cord is no exception. When it occurs, therefore, it is obvious that after the cortex has been roused to discharge, thus evoking the tonic stage, it possesses the power of again emitting impulses when thrown into a high state of excitation. The period at which this clonic discharge commences is variable, there being in some instances a pause or period of delay, whilst in others the intermittent or clonic stage may even overlap the tonic condition, which, consequently, ceases prematurely, while yet the excitation is being continued

The clonic stage, or after effect, has a distinct rhythm (see graphic method, p 273), in which the muscles respond to intermittent impulses. Exactly the same is seen in the electrical changes of the spinal cord. This stage, or after effect, as it truly is, presents three chief features for study.—(1) Its commencement; (2) its development, (3) its mode of termination, these being common to both the muscular and the spinal records

(1) The clonic stage invariably begins with small, often single discharges, *vide* fig 6, these soon increase in strength. This is of course closely imitated by the graphic records of the muscle, the contractions of which, minimal at first, become, later, maximal

(2) The further development of the stage is marked by summation of the impulses, the rhythm of which, directly measured, appears to be about 10 per sec, but we have not yet had time to thoroughly investigate this point. (*Vide* graphic method, p. 273)

The summation of the electrical variations very obviously harmonises with all the other facts relating to the persistence of the muscular contraction, when produced by cortical stimulation. (See also FRANÇOIS FRANCK and BUBNOFF and HEIDENHAIN, *loc cit*)

(3.) The termination of the series of intermittent variations is marked by their becoming fewer, larger, and finally ceasing abruptly (*vide* fig 6), very rarely diminishing to final disappearance.

\* WEDENSKII, 'Archives de Physiologie Normale et Pathol.' (BROWN-SÉQUARD), Jan, 1891.

The absolute values obtained in the electrometer varied in the two stages, as estimated by the eye, and the rough estimate thus formed is supported by the better evidence of the photographs. They average 2 divisions, rarely 3 divisions for the tonic stage, and 1.5 divisions for the clonic stage.

It would appear that this is true for the Carnivorous animal, as represented by the Cat (eleven animals observed). Whether these electrometer figures are the same for the Monkey we are unable to say, as we devoted our attention in the experiments on that higher Mammal (seven animals observed) to photographing the results.

The absolute electromotive values obtained by the electrometer and recorded photographically, are being examined by Mr G F BURCH at the present time, and we, therefore, will postpone the further consideration of this most important point.

(b) *Effects seen in the Galvanometer.*

The total effect produced in the galvanometer when it is connected with the spinal cord, and the cortex is excited, resembles the records of the muscular contractions, in that there are two distinct stages. It need, however, hardly be said that the slow swing of the galvanometer needle is incapable of recording intermittently, and consequently both stages are composed of a series of summated effects. The rate of movement of the needle is notably different in the two stages, and the close observation of this feature proved of much value in other experiments, notably those on the corona radiata, see p. 337.

In the first stage the needle generally begins to move soon after the commencement of the cortical excitation (see Method, p. 299), but often owing to one of the depressing circumstances mentioned on p. 272, the cortex is not normally excitable and the effect it produces when stimulated is consequently delayed. The needle swings steadily during the excitation, but when this ceases there is a distinct check,\* and then as the after-effect develops the needle slowly swings on and gradually comes to a standstill at the end of the second stage or after effect. The mode of termination of this last is slow and deliberate in its gradual diminution, thus contrasting markedly with the abrupt cessation of the galvanometer excursion, when the corona radiata or spinal cord is excited. This gradual dying out of the effect is so absolutely characteristic of the cortex that it can be used for differentiation.

Though well aware of the small value to be attached to the quantitative use of the galvanometric readings thus obtained, we venture to add a few remarks on these in view of the novelty of the point.

When the central end of the whole cord is connected with the galvanometer, and

\* What is said on p. 299, &c, relating to possible errors and fallacies may be here remembered as showing that this check is purely a physiological phenomenon, there being no possibility of the excitation current affecting the delicate galvanometer.

one cortex (*i.e.*, lower limb focus) excited for a definite period, an electrical excitatory variation is produced in the cord, the amount of which is indicated by the following average of several observations

	Duration of excitation	Average strength of excitation	Average variation.
Cat	5 seconds	8500	193°
Monkey	3.5 "	4500	175°

The brain of the Monkey was stimulated for a shorter time, and with far weaker excitation than that used for the Cat, in consequence of our desire not to make the cortex hyperexcitable. Even then the excitatory effect in the Monkey is nearly as large as that in the Cat. The truth of this position is also evidenced by numerous observations we have made under other circumstances, the Cat always requiring a stimulus, which in the Monkey would have evoked a far higher excitatory effect. As with all results obtained by the method of averages, no doubt this point would repay accumulation of observations, since, although no absolute value can be given to the figures, they seem to show specific differences. With the cord divided longitudinally, and the excitatory effect observed in each half, this absolute difference apparently disappears (see p. 354).

Before proceeding further, it is essential that we should indicate the experimental evidence on which we base our interpretation of the electrical changes in the cord.

That the changes are due to the discharge of excitatory impulses from the cortex is clear, but it may be asked what evidence apart from the parallelism discussed on p. 324 there is to show that they are the concomitants of the passage of actual nerve impulses through the portion of exposed cord, and not the results of conduction from the electrical changes evoked in all the surrounding muscles which are thrown into spasm.

The evidence which shows that the change is one localised in the nerve fibres of the exposed cord may be grouped as follows —

(1.) The position of the electrodes being arranged to ensure isolation, as described in Chapter III, p. 295, this isolation is sufficiently complete to allow of the surrounding muscles being thrown into activity without any electrical change in the exposed tract being evident in the galvanometer.

(2.) In observations made in the Monkey with the freshly exposed cortex, the initial and immediately succeeding stimulations of the lower limb area evoked effects which, with the strength of the stimulus employed, were so exactly circumscribed that, since the cord was divided and the lower limbs thus cut off, no demonstrable

muscular movement of any kind existed, yet a marked and distinct electrical change of the usual kind was present in the cord and evidenced both in the electrometer and the galvanometer

When, further, owing to prolonged excitation, exposure, or slighter degree of etherisation, hyperexcitability of the cortex became established, subsequent excitation evoked a more general discharge, and although the muscles of the trunk and upper limb were now thrown into active contraction, the change evidenced by the electrometer and galvanometer remained similar in character to that previously observed

(3) If in any given instance with the central end of the spinal cord in the lower dorsal region exposed and connected with the galvanometer electrodes, the cortical area for the upper limb was excited, no effect was observed in the galvanometer and electrometer, although the muscles of the upper limb were thrown into convulsion

(4) The injury (cutting off, &c.) of the cord between the exposed region and its deep connections abolishes the effect in the cord, even although the muscles are thrown by cortical excitation into violent spasm

(5) In addition to the above, the whole mass of results to be detailed in this and the succeeding chapters is convincing evidence of the truth of our interpretation, since, as will be seen by separating the fibres in the two sides of the cord (longitudinal section), by interrupting the fibres on one side only (hemisection), &c., we obtained a differentiation in our results which admits of no other explanation than the one upon which we base our deductions, namely, that the electrical effects observed are due to changes localised in the exposed cord, and, moreover, in the experiments under discussion localised particularly in the nerve fibres which form the pyramidal tracts

The fact above alluded to of the absence of electrical effects in the dorsal cord when the area for the upper limb was excited in the Monkey, involves matters of such importance that we now pass on to consider it in some detail

#### (c.) *The Localisation of Efferent Representation in the Cortex as ascertained by the Electrical Method.*

It was clear from the commencement of this research, that our method afforded means of differentiating the centres in the cortex and their correlated fibres in the spinal cord. We accordingly made observations of the following character.—

Having exposed the cortex freely, and connected, as before, the cut dorsal cord with the electrometer, we proceeded to obtain the usual result by exciting the lower limb area with a minimal but adequate stimulus, evoking thus an effect without at the same time developing an epileptic hyperexcitability of the cortex. We then explored the rest of the surface of the so-called motor region with the electrodes and the same strength of excitation, to see how far we could determine whether there was

any electrical change in the cord, *i.e.*, the pyramidal tract, really belonging to the lower limb, when other parts of the cortex were excited. As will be now shown, our instrument gave no indications of such diffused effects, but in this relation we must draw attention to the animals used (Cat and Monkey)

Considering that the minute differentiation of efferent motor function in the cortex of the Cat is relatively insignificant compared to that in the Monkey, we employed the former animal for the preliminary investigation of the accuracy of the general position which is involved in our first statements. But we also found in the Cat that, while with a given strength of excitation, stimulation of the lower limb cortical area gave the definite result of a movement of two divisions in the electrometer (the connection of the cord, &c, being as stated before), the excitation of the occipital lobe and the temporo-sphenoidal lobe respectively gave no result at all. Upon this point it may be remarked that in some instances we were able in the Cat even to differentiate, as we easily could do in the Monkey, between the upper limb and the lower limb areas. That is to say, that if the dorsal cord were observed, we got a well-marked effect by exciting the lower limb focus (as indicated by FERRIER), whereas excitation of the fore limb focus produced no visible change in the cord's state, as evidenced by the electrometer.

Thus the following facts were noted in the Cat (126)

CORD led off at Lower Dorsal Region.

Regions of cortex excited	Strength of excitation	Effect in Electrometer	
		Tonic stage	Clonic stage
(a) Lower limb focus	10,000	Rise 2 divisions	1.5 divisions
(b) Occipital lobe	10,000	Nil	Nil
(c) Temporo-sphenoidal lobe	10,000	Nil	Nil
(d) Fore limb focus	10,000	Nil	Nil
For the points <i>a</i> , <i>b</i> , <i>c</i> , <i>d</i> excited, see Plate 30			

Turning now to the Monkey, we carried this mode of investigation still further by the employment of minimal stimuli. The following general result was obtained. The dorsal cord being observed, the greatest effect was produced when the excitation was applied to the centre of the lower limb area, *i.e.*, just at the hallux focus,\* and this effect diminished as the electrodes were removed from that point towards the mesial surface of the hemisphere or downwards over the convex surface towards the superior frontal sulcus. (See Plate 32.) It was interesting to observe that opposite this sulcus,

\* BEEVOR and HORSLEY, 'Phil Trans.,' 1890, &c

where, according to BEEVOR and one of us, the upper and lower limb areas tend to overlap, with the same stimulus as in the latter case this region was the last from which any effect could be produced in the fibres of the dorsal cord. Even in the case where the whole cortex was very excitable, and where a generalised effect was thus easily evoked, and where, consequently, electrical effects in the cord followed stimulation of the upper third of the upper limb area, the general effect was, nevertheless, most markedly graduated from the centre of the lower limb area in diminishing order as the electrodes were removed downwards and passed the level of the superior frontal sulcus.

We may now allude to the obvious inference that might be drawn from these experiments, namely, that although there is no sharply marked line of demarcation between the cortical foci, there is nevertheless in the facts we have just stated a certain amount of evidence against the assumption that the lower limb, for example, is represented to any marked degree in the upper limb area of the cortex. We do not speak with great positiveness on this point, because it may well be that the instrument we chiefly used in this branch of our work, the electrometer, was not sufficiently delicate to show the extremely minute variation which might be supposed to result from the excitation of only a very few fibres. That this indeed seems probable is shown by the results of two experiments which we performed with the galvanometer instead of the electrometer. Unfortunately, however, they do not enable us to speak with greater certainty in the directions indicated, because in each instance the cortex was hyperexcitable from the commencement of the experiment. This, however, is clearly a branch of enquiry which might with advantage be followed out by subsequent observers.

In this connection the experiments of SHERRINGTON\* are very suggestive, and we shall refer again to this part of the subject in describing our experiments on bilateral representation.

(d) *The Amount of the Galvanometric Readings.*

Although, as has been stated, no exact comparison for quantitative purposes can be made between different deflections of the galvanometer, when, being connected with the central end of the exposed spinal cord, the cortex is excited, yet the amounts of the different readings are in themselves of great interest, owing to the fact that it is always possible with an excitable cortex and a sufficiently strong excitation to obtain very large galvanometric deflections. It is obvious that the deflection is dependent not merely upon the intensity but the duration of the stimulation, hence the excitation was limited by the revolving key, previously described, to 5 seconds. Since, however, the cortical discharge lasts a variable time after the stimulus has ceased,

\* 'Proceedings of the Physiological Society,' 1890.



the galvanometric effects display, as might be expected, great inequalities, these, however, will be seen to be in strict relation with the amount of visible contraction evidenced in the muscles of the trunk, &c, and hence are really determined by the force and duration of the cortical discharge. Bearing this in mind, the following table is very instructive, as indicating the size of the deflections, which vary, as is seen, from 63 to 510 scale. The intensity of the stimulus, the particular cortex excited, and the character of the fit evoked, are in each case noted.

It will be seen that the average of these readings, which were all taken in four animals (Cat), as far as possible under similar conditions of etherisation, &c, amounts to 193 scale. It will be also seen that it is always easy to produce by a sufficient intensity of stimulation readings which are in excess of this.

#### GALVANOMETRIC Effects produced in Spinal Cord of Cat by Cortical Excitation

	Intensity of Excitation		Galvanometric Effect	Muscular Movement
Cat (315)	8,000	5'' left cortex	63	Slight fit
	8,000	„ right „	115	„ „
	9,000	„ left „	108	„ „
	9,000	„ right „	230	Good fit
„ (317)	8,000	„ left „	50	Very slight fit
	10,000	„ „ „	162	Fair fit
	12,000	„ „ „	235	Good fit
	8,000	„ right „	130	Slight fit
	10,000	„ „ „	185	Fair fit
	12,000	„ „ „	230	Good fit
„ (319)	10,000	„ left „	90	Slight fit
	12,000	„ „ „	170	Fair fit
	10,000	„ right „	150	„ „
	12,000	„ „ „	260	Good fit
„ (324)	6,000	„ left „	260	Slight fit
	8,000	„ „ „	340	Fair fit
	10,000	„ „ „	510	Powerful fit
			17 = 3288	
		Average	193	

The interest of the results will increase when we compare the average amount with the highest obtainable value of the galvanometric reading afforded by the effect of cortical excitation in the sciatic nerve. It must be now pointed out that in all cases, it is essential to reject observations in which there are sudden irregular changes in the resting electrical difference of the cord, since these are in great measure due to slight failure of the anæsthesia and to the consequent semi-voluntary discharge of cortical impulses.



(e) *Electrical Change in Cord produced by "Semi-voluntary" Cortical Discharges.*

During prolonged etherisation it is well known that animals of all kinds, including Human beings, occasionally make unconscious, but semi-voluntary, purposive movements. These movements are abolished by very profound anæsthesia

Electrical effects manifest themselves in the observed portion of exposed spinal cord when these semi-voluntary movements occur in the upper limb and trunk muscles. The effects are evidenced in the galvanometer connected with the tissue by deflections, which, though resembling the excitatory variations in being always opposed in sign to that of the resting difference, vary very much in amount and rapidity of development. It is obvious that the excitability of the cortex and the intensity of the exciting agency, must be the chief agents in determining the amount of this effect. The extent of such a deflection when, as evidenced by well-marked movements of the muscles on both sides in the upper half of the body, a considerable cortical discharge of energy was taking place, has amounted in the Monkey to 360 scale, it was however, at once abolished by profound anæsthetisation. As a rule the deflections amounted to from 20 to 60 scale, no doubt they would have been larger, had it not been for the fact that, since their appearance interfered with accurate observation of cortical effects evoked by stimulation, we always took care on perceiving them to so alter our conditions of anæsthesia as to abolish this source of error.

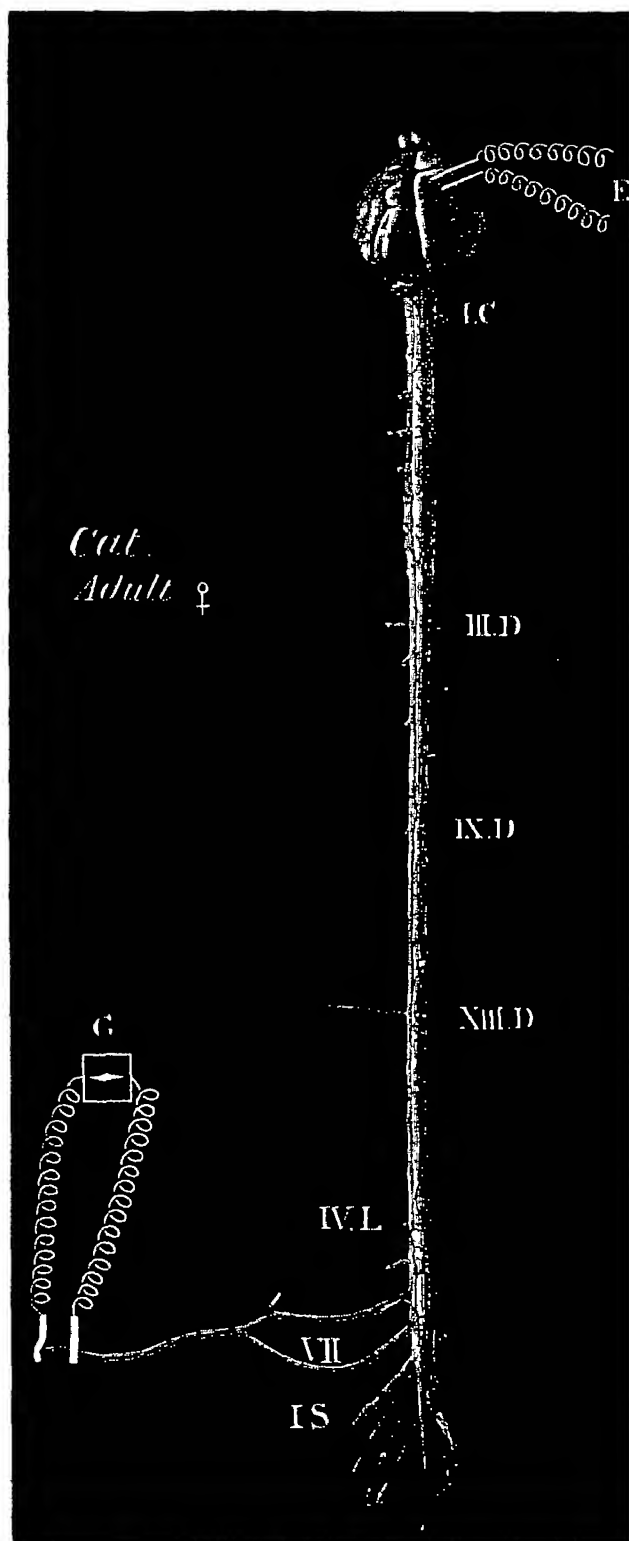
## 2 *Electrical Changes in the Sciatic Nerve*

After having thus considered the electrical changes produced in the spinal cord by the functional activity of the cortex, we next turned our attention to the more complex question of what occurs in the peripheral nerves when the cortex is excited. This is obviously more complex, because, although we are still exciting the cortex, we have now introduced into the mechanism the bulbo-spinal system of centres, so that we are brought at once face to face with the question as to how far the changes which we have just been studying in the spinal cord are modified by the as yet hypothetical termination of the fibres of the pyramidal tract in the said bulbo-spinal centres.

We are justified in expressing this query in a still simpler fashion: what becomes of the cortical impulses when they reach the bulbo-spinal centres? Other things being equal, it might have been expected that we should have got very clear evidence of the effect of active excitatory change in the peripheral nerve, seeing that if this had been still in connection with the muscle, the muscle would have been thrown into a powerful series of contractions. It was, therefore, with very considerable surprise that we observed what a relatively small electrical variation was obtainable in the sciatic nerve when the corresponding portion of the cortex was excited. The experimental procedure was extremely simple, and as follows.—The cortex was exposed, as and the sciatic nerve on the opposite side of the body was also exposed,

ligatured, divided below the ligature, and its central end connected in the manner indicated in Chapter III. with the galvanometer or electrometer electrodes. (See fig 7 )

Fig 7



We found that excitation of the cortex in most cases produced no perceptible effects when the capillary electrometer was in connection with the nerve, and when occasionally effects were seen, their complete absence in other instances, and their rapid disappearance on repetition, threw doubt on the observations.

With the galvanometer, however, effects could always be seen, though these were very small in amount as compared with those observed in the spinal cord. In a few cases, however, in which the excitation applied to the cortex was very intense, so

as to arouse very violent and prolonged bilateral fits, the deflections observed approached in size the smallest of those obtained in the cord. The general results will be seen by the following table, in which the effects observed in the nerve on the opposite (*i.e.*, corresponding) side to the excited cortex of eleven Cats and two Monkeys are separated from those observed in the nerve on the same side. The table is so arranged that the weak fits are given first and the stronger prolonged ones last.

It will be seen that the amount of deflection varies from a mere trace to 80, the larger readings being always obtained in the case of powerful prolonged and bilateral fits. The average of all the readings in the nerve opposite to the excited cortex is 31, whilst under no circumstances, even with the most powerful fits, is an effect obtained equal in amount to the change evoked in the spinal cord.

	Intensity of Excitation	Duration of Excitation	Effect in Nerve Opposite to Cortex.	Effect in Nerve on same Side as Cortex	Character of Fit
		Secs			
Cat (291)	12,500	5	2		Weak
" (293)	10,000	"	7		"
			6		"
" (296)	11,000	"	5		"
			9		"
			12		Slight
			20		Fair
" (299)	12,000	"	12	10	Weak
			20	.	Fair
			10		"
" (290)	"	"	18	2	"
			10	.	"
			22		"
" (71)	6,000		20		"
Monkey (54)	5,000	3½	16	5	Good
			18	1	"
" (217)	"	"	28	18	"
			18	..	Moderate
			16	5	"
Cat (298)	12 500	"	28	.	Good
" (75)	"	"	35		"
			28		"
	10,000	"	35	..	Violent
			55		Prolonged
" (292)	12,500	"	62		} Prolonged powerful fits
			46		
			80		
" (79)	"	"	"	.	} Prolonged powerful fits
" (301)	12,000	"	70	80	
					Prolonged powerful fits (morphia)
			28=868		
		Average	31		

If we select out of the whole table those readings which were obtained with fits of a unilateral character, thus disregarding the whole of the larger numbers, we find that the average amounts to 20, this being very much below the average unilateral effect in the cord (See Chapter VII)

It might be imagined that this difference in amount between the nerve and cord effect was entirely connected with the difference in sectional area and thus in resistance, that this is not the case is shown by the following considerations —

(a) The total resistance in connection with the preparation is made up of the electrodes with their cables and the tract of tissues, of these the resistance of the cables is far in excess of that of the tissue, and hence any difference in resistance between the spinal cord and nerve preparations due to the sectional area of the tissue is but a small fraction of the whole

(b) The absence of effect in the capillary electrometer, when connected with the nerve, shows that any unusual resistance which may be offered by the nerve as compared with the cord is not the cause of the diminution, since the amount of the electrometer movement is unaffected by changes of resistance

(c) The sectional area of the nerve of an adult large Cat is nearly as great as that of the dorsal cord of a young animal or a small Monkey, yet the effect is small in the former and large in the latter structure

(d.) As will be seen in Chapter VII, on bilaterality of representation, it is possible to obtain large effects in only one-half of the cord, split longitudinally. This portion has apparently less sectional area than the sciatic nerve, but the electrical change in it, as will be seen by reference to the tables, is far in excess of the nerve change.

(e.) The change in the cord is undoubtedly one connected with the fibres of the pyramidal tracts, it is therefore with reference to their sectional area as compared with the area of the motor nerves in the sciatic nerve that any criticism on this head should be directed. There is, however, every reason for supposing that the pyramidal tracts in the dorsal region are smaller in cross section than the sum of the anterior roots of the lumbar plexus.

These considerations serve to emphasize the conclusion to which, as it appears to us, the foregoing results tend, viz, that the extraordinary difference in quantity between the electrical effect in the cord and in the sciatic nerve when the cortex is excited, must be attributed to an alteration in the quality and quantity of the nerve impulses in their passage from the cord into the nerve, and that the structure of the spinal centres, through which the impulses must necessarily pass to reach the issuing nerves, so influences the transmission as to cause this striking change. This view is strengthened by the remarkable confirmation which is given to it by experiments in which both the spinal cord is directly excited and the centres in it discharged reflexly by stimulating its posterior roots. It will be seen (Chapter X., p 478, and Chapter XI., p. 494) that under these circumstances the electrical effects produced in the sciatic nerve are extremely small and resemble in amount those above referred to.

The largest effects we have ever seen in the nerve in consequence of cortical excitation have been obtained by the use of absinthe. The powerful general fits which followed the introduction into the blood of this drug being evidenced in two animals (Cat) by effects which have amounted to 272 scale. It need hardly be pointed out that such fits are of extremely prolonged character, and that in the spinal cord electrical changes occur which give deflections in very many cases too large to be read (off screen).

### *Cortical Localisation as Evidenced by Electrical Changes in the Nerve*

The electrical changes in the nerve, as evidenced by the galvanometer, although small, are quite definite, and afford additional proof of the localisation of cerebral representation. Thus, when an adequate stimulus was employed, which was, however, only intense enough to evoke unilateral muscular contractions, the electrical change in the nerve was entirely confined to that on the opposite side to the excited cortex. This subject will be discussed in detail in Chapter VII, which deals with bilaterality of representation. It may, however, be pointed out that no other operative interference than that already described as necessary for cortex and nerve exposure having been performed, it is perfectly evident that if the stimulus was maximal, as it usually was in this experiment, a bilateral fit could and did happen, so that from one nerve an effect might be and was obtained due to discharge of both hemispheres.

It is, moreover, interesting from the point of view both of control and of localisation, that in cases where a strength of stimulus which did not evoke a general discharge was employed, whilst the application of the stimulus to the so-called lower limb area of the Cat produced definite electrical changes in the nerve, its application to the focus of representation of the upper limb evoked little or no change, even though the stimulus was followed by marked epileptic convulsions in the upper limbs. The localisation of the foci of representation of the movements of upper and lower limbs in the Carnivora, which has been determined by other observers, is thus corroborated by the use of the present method.

## CHAPTER VI —ON THE ELECTRICAL EFFECTS EVOKED IN THE SPINAL CORD AND MIXED NERVES BY EXCITATION OF THE CORONA RADIATA

### EXCITATION OF CORONA RADIATA

#### 1. *Electrical Changes in the Spinal Cord.*

We will consider first the general character of the changes as evidenced by the ~~movement of the capillary electrometer.~~

*(a) Effects seen in Electrometer*

The cortex and spinal cord having been exposed, the central end of the cord divided in the lower dorsal region was connected with the instrument in the manner already described, and the corona radiata displayed by the method detailed in Chapter III, Section 2.

We have already stated that it was early shown by FRANÇOIS FRANCK and others that removal of the cortex and excitation of the corona radiata no longer gave the characteristic sequence of tonic followed by clonic muscular contraction, but simply a tonic contraction synchronous with the duration of the excitation, the first stage, as it were, of the cortical effect. . In our earliest experiments (see 'Roy. Soc. Proc'), we found that a similar difference occurred in the character of the electrical changes observed in the spinal cord, as evidenced by the capillary electrometer. The character of the change in the two conditions is well shown in the facsimile representations of the photographic records which are given in our former paper, the corona radiata effect being simply a persistent tonic negative variation, the amount of movement of the meniscus being about one division of the eye-piece scale.

The small size of the electrometer change, and the consequent difficulty of appreciating its comparative quantitative value under different circumstances, led us to employ the galvanometer as an index of its amount

*(b.) Effects seen in Galvanometer.*

When the effect in the cord is observed with this instrument it is seen to be unlike that evoked by cortical excitation in this respect, that the deflection of the needle commences with the application of the stimulus, and ends sharply with its termination. The amount of the deflection is thus very definite, but of less extent than that obtained when the cortex is excited

In the following table a series of observations made on three Cats are given, in which precautions were taken to insure that the state of anæsthesia, &c., should be in all cases as far as possible the same. The deflections vary from 37 to 175, the average being 102.

## EFFECT in Spinal Cord

	Intensity of excitation	Duration of excitation	Effect in spinal cord	Character of muscular effect
Cat (99)	12,500	Secs 5	42	Tonic contraction
			37	" "
			50	" "
" (288)	10,000	5	118	Well marked tonic contraction
			58	" " "
			120	" " "
			62	" " "
	11,000	5	130	Well marked tonic contraction
			110	" " "
			71	" " "
			170	" " "
" (309)	8,000	5	125	Well marked tonic contraction
			175	" " "
	8,000	5	135	" " "
			129	" " "
			15=1532	
		Average	102	

We would pass from this part of our subject, since our knowledge of the process of secondary degeneration has shown that in the arrangement of the experiment all we do is to observe at one (the spinal) end of a column of fibres the changes evoked by stimulating these fibres at the other (corona radiata) end, were it not that the above effect is capable of modification in a manner which demands consideration. Moreover, we wish to emphasise the fact, that in its simplest form the corona radiata effect, as observed in the cord, is an example of the application of the galvanometric method to the determination of directly continuous nerve tracts in the central nervous system. This, as we shall see later in dealing with the spinal cord itself, is one of the most valuable uses to which the method can be put. Thus when a definite tonic effect, and that only, is evoked by the excitation, the application of the stimulus to any fibres of the corona radiata, except those immediately underlying the focus of representation of the movement of the lower limb, produces no electrical changes in the lower dorsal cord, even though the muscles of other parts are sent into tonic contraction. The modifications we have referred to above, are those which have been observed by most workers with the graphic method, and consist in the presence of an after-effect in no wise differing from the clonic stage of the full cortical discharge save in duration and completeness. The assumption is naturally that in the arrangement of the experiment, it is impossible to avoid exciting association fibres (*fibræ arcuatae*,



&c ), which arouse the neighbouring cortex cerebri, and cause a discharge from corpuscles in which the peripheral part under investigation is yet represented

We have little doubt but that this is the true explanation, and believe that excitation really limited to the fibres of the corona radiata is never followed by such an after-effect. This will, however, be again referred to in Chapter VII

## 2 *Electrical Changes in the Sciatic Nerve*

As in the result of cortical stimulation, so in that of excitation of the corona radiata, there is a striking difference between the effect in the cord and that in the sciatic nerve. We have never yet observed any effect from the nerve when the electrometer was employed, in the galvanometer, however, such effects are generally seen, although the necessary stimulus has to be so strong as to run the risk of evoking discharge from the uninjured portions of cortex. Whenever such epileptic discharges obviously occurred, as evidenced by the muscular movements, the observation was regarded as worthless.

The following table gives the results observed in eight Cats, all those being excluded in which, owing to the degree of anæsthesia being less, the excitation brought about general muscular movements.

As in the case of cortical excitation, so here, the deflections observed in the (corresponding) nerve on the opposite side to that of the excitation are placed in a separate table to those observed in the nerve on the same side, the latter being given so as to show when bilateral effects were produced

It will be seen that the amounts vary between 4 and 68, and that the average of all readings is 26.

## FREDERICAT Effects in the Nerve

	Intensity of excitation	Duration of excitation	Effect in cor- responding nerve	Effect in nerve on same side	Muscular effect observed
		Secs			
Cat (290)	12,000	5	7	0	Tonus only
			9	0	" "
" (291)	12,500	5	5		Weak tonus
" (292)	9,000	5	20	12	Good "
			18		" "
	10,000	5	20		" "
			6	2	" "
" (297)	12,500	5	12	0	Good "
" (298)	12,000	5	4	0	Weak "
	12,700	5	11	0	Good "
" (299)	12,000	5	46	21	Powerful bilateral tonus
			61	26	" " "
			10	0	Weak tonus
" (303)	10,000	5	30	12	Bilateral tonus
			28	14	" "
			22	8	" "
" (305)	8,000	5	52	14	Powerful "
			63	33	Bilateral "
			23	5	Feeble "
	10,000	5	59	25	Good "
			10	1	Very feeble tonus
			31	13	Fair tonus
			68	42	Bilateral good tonus
			23 = 615		
			26		

Special attention must be drawn to the fact that higher numbers than those give were sometimes obtained; however, these large deflections accompanied general movements of the animal, due, in part, to the fact that it is extremely difficult to maintain a proper degree of anaesthesia. If this is too slight, the stimulus causes general awakening of the whole cerebral system.

The question of bilaterality will be referred to in the next chapter. It remains to institute a general comparison between the galvanometric effects observed in both cord and nerve when the cortex and corona radiata are respectively excited. Such comparison will lead to a better understanding of the part played by the bulbo-spinal centres, though any complete inquiry into this difficult question must be postponed to Chapter XI., which treats directly of the matter.

If we arrange the parts of the nervous system here dealt with in their anatomic order, they form the following series:—

Cortex.  
Corona radiata.

3. Spinal cord (dorsal region).
- 4 Bulbo-spinal centres.
- 5 Nerve
- 6 Muscular nerve-endings.

The combinations of these parts involved in our experiments may be grouped as follows, and to each group is affixed the highest and lowest galvanometric reading obtained in the case of the Cat.—

Part stimulated	Part observed	Galvanometric effects		
		Highest	Lowest	Average
1-3 Cortex .	Dorsal cord	510	50	193
1-5 " .	Sciatic nerve	80	2	29
2-3 Corona radiata	Dorsal cord	175	37	102
2-5 " " .	Sciatic nerve	68	4	26

From these figures, which apply to the Cat only, it is very evident that the specific element distinguishing the cortex from the white fibres of the corona radiata leading away from it is the energetic discharge of its own structure, the corpuscles. Reverting now to the question raised at the beginning of this section, it is plain that the average amount of the effect produced by the corona radiata forms practically half, viz, 102, that, viz, 193, evoked by the cortex, the remainder naturally corresponding with the clonic after-effect. The levelling process effected by the block in the connection between the pyramidal fibres and the nerves through the corpuscles of the bulbo-spinal centres is so severe as apparently to reduce the increase due to the after-effect to too low an intensity to make itself felt in the galvanometer in any marked degree, for it will be seen in the above table that the figures for the sciatic nerve are practically equal.

Beyond multiplication of experiments to check and control these observations, we did not see that further investigation in this direction would be so profitable as examining the relations and action of the bulbo-spinal centres when separated from the cervical region of the spinal cord (see Chapters VIII., IX., X, XI), since the phenomena of conduction in fibres are far more easily studied than those in which corpuscular mechanisms are involved.

CHAPTER VII—ON BILATERALITY OF REPRESENTATION IN THE CEREBRUM, AS EVIDENCED BY THE ELECTRICAL CHANGES IN THE SPINAL CORD AND MIXED NERVE

The galvanometric method affords an excellent means of determining to what extent any bilateral movements obtained in the lower limbs on exciting the cortex are associated with impulses proceeding down both sides of the cord.

It is obvious that a most important question is involved in this inquiry, that, namely, of the share taken in the production of bilateral effects by the different parts of the nervous system. When bilateral movements of the lower limbs are evoked by excitation of one cortex, it is conceivable (*a*) that in the portion of cortex excited, muscular movements on both sides are represented, (*b*) that the excitation has aroused the corresponding cortical areas in the opposite hemisphere, and thus produced the bilateral effect, (*c*) that the excitation has aroused the basal ganglia, cerebellum, &c, (*d*) that the descending impulses, although unilateral when they come into relation with the spinal centres, are then brought into relation with both sides of the body.

In order to investigate this, the first problem to solve is that referred to last under (*d*). This, the present method, and that only is capable of doing, since by it we can determine the characters of the actual descending impulses in the cord before they come into relation with the bulbo-spinal centres. In this way we can ascertain to what extent the impulses which descend the cord from the brain already show a dual (bilateral) grouping.

We devoted a very large number of our cortical experiments to the further elucidation of this question, feeling that the great importance of any approach towards its solution, in consideration of its bearing upon the physiological characteristics of the cortical cells, was a sufficient justification.

It is necessary, before stating our results, to give a short categorical account of the work already done in this subject, and this is the more desirable since we cannot find any such *résumé* published.

#### PREVIOUS WORK ON THE SUBJECT.

The question whether both or only the opposite of the two sides of the body are represented in one cortex cerebri on the efferent or motor side has been approached experimentally by relatively but few authors.\* As the results hitherto obtained do not by any means decide the important questions which offer themselves for solution,

\* The subject has also been considered fully from the theoretical point of view by BROADBENT ('British Medical Journal,' 1876, pp. 333, 401), this author believing that bilaterality of representation is always effected by commissures between the bulbo-spinal centres.

it is impossible to tabulate the facts in the definite manner used for the historical retrospect of the graphic and other methods

Moreover, since the interpretation of the results is completely dependent upon the methods of experiment in each case, it will be better to arrange the facts as follows —

- (1.) Excitation experiments on the cortex.
- (2) Excitation experiments combined with division of commissures, *i e*, corpus callosum, &c
- (3) Excitation experiments combined with the excision of the opposite “motor” area
- (4) Excitation experiments combined with hemisection of the spinal cord or bulb
- (5.) Ablation of one hemisphere.
- (6) Ablation of the “motor” area of one hemisphere followed by ablation of that of the opposite side.
- (7) Excitation of the corpus callosum.
- (8.) Degeneration of fibres after excision of portions of the cortex cerebri

We will now briefly state the more important facts determined by the above methods of experiment, postponing for the present any criticism

### 1. *Excitation Experiments on the Cortex*

It was first observed by HITZIG,\* later by FERRIER,† ALBERTONI,‡ and MUNK,§ and subsequently by FRANCK and PITRES,|| that powerful excitation of one hemisphere in the Carnivora produced movement not only of the corresponding or opposite side of the body, but also of the same side as that stimulated.

FRANCK and PITRES|| showed further that when the muscles of the same side were thrown into action they contracted 0.1 second later than those of the opposite side, a most important observation

BUBNOFF and HEIDENHAIN,¶ CARVILLE and DURET,¶ confirmed these facts

JANICKE\*\* observed that while in dogs bilateral representation of the facial muscles was very constant, in the limbs on the contrary, unilaterality was the rule, but that to this there were exceptions His views were confirmed by UNVERRICHT

LEWASCHEW†† noted that the movement on the opposite or corresponding side was a coordinated one (like a voluntary action), whereas that of the same side, besides being late, was only a simple tonus

\* ‘Untersuchungen uber das Gehirn,’ Berlin, 1874, pp 48, 134

† ‘Functions of the Brain,’ 1st ed, 1874

‡ ‘Lo Sperimentale,’ 1876

§ ‘Gesammelte Abhandlungen,’ 1890

|| ‘Compt Rend Laboratoire,’ MAREY, 1878, 1879.

¶ *Loc. cit*

\*\* ‘Centralblatt fur klinische Medicin,’ March, 1883, p 177.

†† *Loc cit* See p 346, *infra*.

SCHAFER and HORSLEY\* noted that bilateral representation of the facial muscles existed in various species of Monkey, but that the trunk and limb muscles were unilaterally represented.

SCHAFER and MOTT† confirmed these observations

BEEVOR and HORSLEY‡ further showed in more detail that in the Bonnet Monkey (*Macacus sinicus*) the limbs were unilaterally represented, but that other groups of muscles, *e.g.*, the tongue, buccinator oris, &c., &c., were bilaterally represented in each hemisphere. They discuss this point also in another Paper on excitation of the internal capsule,§ and confirm the above statement relating to the trunk muscles.

SEMON and HORSLEY|| have shown that in all animals the vocal cord movements are absolutely bilaterally represented in the excitable area of the cortex, this bilaterality was previously observed by KRAUSE in the Dog, it has been contested by MASINI.

BROWN-SÉQUARD¶ in one experiment on a Monkey found that excitation of the gyrus fornicatus produced movements of the same side of the body, whereas excitation of the paracentral lobule immediately above evoked movement of the *opposite* side.

ASCH and NEISSER\*\* found from (but a few) experiments in Rabbits that excitation of the cortex produced movement of the muscles on the same side, and, subsequently, those of the opposite side, whereas excitation of the corona radiata gave movement on the opposite side. The narcosis in their experiments was incomplete.

COUTY†† occasionally also observed the same phenomenon exceptionally in Rodents, but only in the absence of narcosis. STEFFAHNY‡‡ observed occasionally bilaterality of movement in Rabbits to follow excitation of one hemisphere. BRAUN§§ similarly noted bilaterality in the absence of narcosis.

## 2. *Excitation Experiments on the Cortex combined with Division of Commissures,* *i.e., Corpus Callosum, &c.*

EXNER||| observed that in the Rabbit, after section of the commissures, and even after ablation of one hemisphere (see No. 5), bilateral movements (nature not detailed, possibly tonus, p. 189 of his paper), occurred.

\* 'Phil Trans,' B., 1888.

† 'Brit Med. Jour,' 1890.

‡ 'Phil Trans.,' B, 1887, 1888, 1890

§ 'Phil. Trans.,' B, 1890

|| 'Phil. Trans,' B, 1890

¶ 'Comptes Rendus de la Société de Biologie,' 1887, p. 261

\*\* 'Archiv für d. ges. Physiologie,' von PFLÜGER, 1887, p. 191.

†† 'Compt Rend.,' vol. 96, 1883, p. 506.

‡‡ ECKHARD'S 'Beiträge,' 1888, p. 97.

§§ ECKHARD'S 'Beiträge,' 1876, p. 127.

||| 'Wien, Akad Sitzber,' 1881, 3 Abth., p. 185.

FRANÇOIS FRANCK and PITRES\* found that in the Dog, after division of the corpus callosum, the anterior and middle commissures, or even the pons, “les réactions bilatérales” persisted (? tonus only)

GLIKY† also found (see No. 4) bilaterality of movement after dividing all parts in the middle line to the mesencephalon, in the Rabbit.

HORSLEY‡ showed that in the Dog after division of the corpus callosum and commissures, as described by FRANCK and PITRES, although bilateral movements could be obtained upon excitation of one hemisphere, yet the movements were not the same in character on the two sides, the true cortical effect of tonus followed by clonus being only obtainable in the side opposite the excitation, whilst the effect on the same side was only a feeble tonus (*vide* also LEWASCHEW) and often absent

### 3 *Excitation Experiments on the Cortex combined with Excision of the Opposite “Motor” Area*

FRANCK and PITRES§ observed in the Dog the bilateral movements to persist (? tonus only on the same side) even after the opposite motor area had been removed (“centres corticaux opposés au centre excité”), and EXNER|| also in the Rabbit noted the occurrence of bilateral movements if one hemisphere were excited, even when the whole or major part of the opposite one had been excised

HORSLEY¶ found the same in the Dog, but noted that while the limbs opposite (*i.e.*, corresponding) to the side excited developed the usual combination of tonus followed by clonus, the limbs on the same side exhibited only tonus. Further, that as in Nos 1 and 2 the complete (tonic *plus* clonic) discharge from the cortex of one hemisphere could be obtained by adequate excitation without any bilateral movement whatever.

He also found the same to be true when the excitable region of one hemisphere was ablated and absinthe injected into a vein. In the resulting epileptic convulsion only tonus was noticeable in the limbs corresponding to the seat of ablation, whereas the typical tonus *plus* clonus was exceedingly marked in the limbs opposite the sound hemisphere. This differentiation was often very precise, *i.e.*, the tonus on the side of the sound cortex was very weak, even in the Cat

In the Monkey the tonus mentioned was extremely slight, and possibly in Man is absent (OBRE) under these circumstances.

\* *Loc cit*

† ECKHARD'S 'Beitrag,' vol 7, p 179, 1876

‡ 'Brown Lectures and Reports'

§ See for full discussion FRANÇOIS FRANCK 'Fonctions Motrices du Cerveau,' 1887, p 59

|| *Loc cit*

¶ 'Brown Lectures' since 1885, also, 'Reports of the Brown Institution.'



SEMON and HORSLEY\* observed that in all animals examined, *i.e.*, Rabbit, Cat, Dog, and Monkey, the bilateral movements of the vocal cords were still perfectly obtained on excitation of the one cortical representation after that of the opposite side had been removed

#### 4. *Excitation Experiments on the Cortex combined with Hemisection of the Spinal Cord, &c* (ECKHARD'S Method)

FRANCK and PITREST† observed that in the Dog hemisection of the spinal cord on the same side as that of the hemisphere excited failed to abolish the bilateral movements in the limbs

LEWASCHEW‡ followed the French authors by similar experiments in the Dog, from which he deduced the same idea, *viz.*, that the bilaterality was accomplished by means of commissural fibres in the spinal cord

BALIGHIAN§ observed that in the Rabbit the opposite, *i.e.*, normally corresponding, movements were not abolished by hemisection of the bulb opposite the lower border of the pons and on the same side as that of the hemisphere excited, whence he concluded that the crossing of the excitable fibres begins to occur as high as the lower border of the pons

BALIGHIAN also showed that in the Rabbit, excitation of one hemisphere failed to elicit movement in the opposite limbs if the corresponding part of the spinal cord had been divided

SCHIFF|| found that in the Dog after section of the right crossed pyramidal tract excitation of the cortex with four Leclanché elements produced no result (whereas before the division this formed a maximal stimulus), and only with a current of fourteen elements were movements of both the hind limbs obtained.

GLIKY¶ showed by hemisection of the bulb that in the Rabbit the pyramidal tract crossed below the centre of the fourth ventricle, and that a tendency towards unilaterality of representation prevailed.

STEFFAHNY,\*\* applying this method in Rabbits, came to the following conclusions: that the path of the crossed impulses for the innervation of the extensors of the fore limb is in the uppermost part of the cervical cord, the anterior column, and lower down in the lateral column, and further that there are paths for bilateral movements, and that these lie in close relation to those for the ordinary crossed effect.

\* *Loc cit*

† *Loc cit*

‡ PFLUGER'S 'Archiv für die gesammte Physiologie,' vol. 26, 1885, p. 279

§ ECKHARD'S 'Beiträge,' vol. 7, 1875

|| PFLUGER'S 'Archiv,' vol. 30, 1883, p. 248

¶ ECKHARD'S 'Beiträge,' vol. 7, 1876, p. 186

\*\* ECKHARD'S 'Beiträge,' vol. 12, 1888, p. 43.

SCHIFF,\* by limited section of the parts of the cord, was the first to find that after division of the crossed pyramidal tract in Dogs, no movement of the leg on the same side as the lesion followed upon excitation of the opposite excitable area

DUPUY† stated that in the Dog opposed hemisections of the cervical region of the cord when separated from each other by about 1–1.5 cm did not interfere with the production of movements in the lower limbs on exciting the cortex cerebri

### 5 *Ablation of one Hemisphere*

To test localisation in principle GOLTZ‡ has in the Dog removed large proportions of the brain, and recently§ succeeded in completing the ablation of one hemisphere

The animal under these circumstances could walk, run, and use the limbs in all automatic movements of feeding, &c, there being no obvious persistent hemiplegia as in Monkeys and Men. For many weeks, however, there is in the Carnivora marked hemiplegia of the opposite side to the lesion (all authors), and according to HIRTZIG the loss of the “muscular sense” is permanent in these animals. This fact, as well as the concomitant persistence of anæsthesia to moderate tactile impressions, is also confirmed by the observations of SCHIFF, and one of us (V H)

SEMON and HORSLEY|| found that in all animals examined after removal of one hemisphere the “automatic” i.e., respiratory, movements of the vocal cords were perfectly bilateral

### 6 *Ablation of the “Motor” Area of one Hemisphere, followed by Ablation of that of the Opposite Side.*

CARVILLE and DURET¶ investigated the matter by removing one so-called motor area, and observing the paresis caused thereby, noting that the paresis gradually disappeared as if by substitution on the part of the opposite sound hemisphere. Removal of this latter, however, did not reproduce the paresis of the limbs on the same side

### 7. *Excitation and Degeneration of the Corpus Callosum*

The results of excitation of the corpus callosum by SCHAFER and MOTT,\*\* as well as the degeneration observed by SHERRINGTON†† to follow localised ablation of portions

\* ‘Archiv f d ges Physiologie,’ vol 30, p 248

† ‘Compt Rend Soc de Biol’

‡ “Verrichtungen des Grosshirns” PFLUGER’S ‘Archiv,’ vol 34, 1883, p 50

§ Demonstration at the 1st Internat Physiol Congress, Basle, 1889 See also the full account given by LANGLEY and GRUNBAUM, ‘Journal of Physiology,’ vol 11, 1890.

|| *Loc cit*

¶ ‘Archives de Physiologie’ (Paris), 1875, p 446, &c

\*\* ‘British Medical Journal,’ 1890, also ‘Brain,’ 1890

†† ‘Proceedings of the Physiological Society,’ 1889

of one cortex, suggest that the corpus callosum is a true commissure between the excitable or "motor" areas

BROWN-SÉQUARD\* had previously shown that the corpus callosum was excitable about its middle third, and he consequently regarded its fibres as commissural between the hemispheres

### 8 *Degeneration of Fibres after Excision of Portions of the Cortex Cerebri*

The phenomenon of bilaterality of function has also been referred to the normal exercise of those fibres which degenerate bilaterally (PITRE†) in the spinal cord after lesion of one hemisphere. Although the degeneration method has established completely the existence of such atrophy of channels in both lateral columns of the cord consequent upon a unilateral cerebral lesion, we do not, unfortunately, know whether these channels are "recrossed," as suggested by SHERRINGTON,‡ CHARCOT, and others, or what is their destination, or whether they are to be regarded as of constant occurrence. As regards the latter point, it is certainly at present considered that they are not constantly affected by a cerebral lesion, and yet more rarely degenerate after a hemisection of the spinal cord. As yet, therefore, the method does not afford anatomical means of deciding the questions at issue.

### RELATION OF THE FOREGOING FACTS TO OUR OWN EXPERIMENTS

In summarising the facts thus collated on this subject, it is difficult to avoid discussing the theoretical interpretations advanced by the authors quoted, but we do not think that anything is to be gained by such a procedure, and intend now to merely point out what conditions yet remain to be satisfied before anything like a full conclusion can be arrived at

All agree that in the intact nervous system a nerve impulse from one hemisphere may readily pass to the other, excite it, and thus bring about bilaterality of movement as a result.

Nothing, however, can be judged as to such crossing to the other hemisphere being necessary for bilateral function until it is clearly defined in which part of the body such functional effects occur

We must for this reason exclude altogether from the present discussion the facial movements, since these§ (see p 344) are in great measure bilaterally repre-

\* 'Compt Rend Soc de Biol,' 1879, p 165, 1881, p 204.

† 'Archives de Physiologie,' 1884, p 142

‡ 'Journal of Physiology,' 1885, p 177 See also summary by TOOTH "Gulstonian Lectures on Secondary Degenerations of the Spinal Cord," 1889.

§ Cf. PAXTH; also UNVERRICHT

sented in the excitable cortical areas of each hemisphere. The question, therefore, narrows itself down to that as to whether the highest, *i.e.*, purposive, movements of the *limbs* of both sides of the body are represented in the cortex of one and the same hemisphere. Theoretically, we are compelled to admit (following the teaching of HUGHLINGS JACKSON) from the evolutionary standpoint such bilateral representation of the limbs. The important point for experiment to decide, however, is whether such bilateral cortical representation exists in more highly differentiated animals to a sufficient extent to cause movements. The opinion of most authors is evidently that it does so exist. We feel, however, very strongly that the methods hitherto adopted by these authors are not definitive, and do not establish the positions claimed. We are led to this conclusion from the consideration of certain facts now to be discussed which have come under our notice in the present research, as well as of others previously discovered, the importance of which has of late become more recognised. By welding the fresh information, which the use of our method has given, to the old, we hope to help forward the solution of this apparently simple but very complex subject.

(1) *Narcosis* —As is seen from the foregoing retrospect, some authors have employed narcosis to a greater or less degree. The statement that a narcotised cortex could in any way “completely discharge” is always, of course, open to objection, and hence observations in animals narcotised to unconsciousness have been held by some to be incomplete. The answer to this objection, however, is simple and, we believe, sufficient; it is included in that of the next paragraph, in which “complete discharge” of the efferent apparatus of the cortex is seen to be effected even in unconsciousness. Clinical experience of epilepsy also affords evidence of the truth of this contention.

To look at the question from the opposite standpoint, although electrical excitation of the cortex is not in any way painful, still it is clear from observation of the influence of such stimuli in imperfect narcosis that the effect spreads rapidly from centre to centre, *i.e.*, to the opposite hemisphere, &c, and hence renders any topographical conclusions impossible.

The observations, therefore, which have been made in this way, though very valuable as throwing much light on synchronous excitation, *e.g.*, in epilepsy, &c, cannot, as yet, form a basis for the determination of the presence or absence of bilaterality of representation so far as the limbs are concerned.

(2) *An adequate stimulus which completely discharges the cortex at one given focus of representation of one limb produces movement in that limb only and none in the limb of the same side*

By the term “adequate stimulus which completely discharges the cortex” at one given spot, we mean an interrupted induction current of sufficient strength to evoke a strong movement in the limb represented (in the present research the leg), and to produce a slight excitation also (by overflow of nerve impulses) of the nearest lying centre or focus, which in our experiments was naturally that for the fore or upper limb. If the strength of the stimulus and the condition of the cortex be accurately

gauged beforehand, so that the latter is not thrown into a hyperexcitable state, then the above mentioned phenomenon can invariably be obtained, and this not only in the Monkey but also in the Cat. It might be objected that the cortex was not completely discharged, but we regard the overflow of the excitatory changes into the neighbouring foci as sufficient evidence of the required completeness. Moreover, the converse position, viz., the appearance of bilaterality tells the same (story see pp 354 and 359), and thus forms the crucial argument.

If we are warranted, therefore, in our view that the cortex under these circumstances is completely discharged, the above described phenomenon negatives the practical existence of bilateral representation of the limb muscles in these animals.

(3.) *When ("bilateral") movements of both limbs follow excitation of one hemisphere after the excitable cortex of the opposite hemisphere has been thrown out of gear by ablation, division of the commissures, &c, &c, the movement of the limb on the side opposite to the cortex excited is the complete cortical effect of tonic followed by clonic contractions, whereas the movement of the limb on the same side as that of the cortex excited is only a tonic contraction.*

If bilateral movements of both limbs receive their originating impulses directly from one cortex, it is not comprehensible why the above-mentioned striking difference in the kind of movement of the limbs should exist. This difference, specially insisted on by one of us,\* has been also observed by several authors (LEWASCHEW, &c), and it suggests that the movement noted on the same side as the excitation is of some origin other than the cortex (its corresponding cortical apparatus being destroyed, be it remembered), for a simple tonus lasting during the excitation is characteristic not only of the cortex but of the cerebellar or other lower centres.

(4.) *When bilateral movements of limbs are observed, those of the limb of the same side as the cortex excited are always later in commencement than those of the opposite side. (FRANCK and PITRES.)*

This delay in movement of the limb of the same side is attributed by most to loss of time in traversing basal commissures. There is no means of testing this view except by some arrangement in which the exclusion of the said commissures is provided. As far as the commissures in the cord are concerned, this might be achieved by ascertaining the time relations of such excitatory electrical changes as will presently be shown to appear in each half of the longitudinally divided cord upon stimulation of the cortex.

(5) *All experiments on this subject have included in their anatomical plan the cerebellum, without excluding its functional influence.*

In our own experiments about to be described, as well as those of the authors already quoted, the cerebellum has been left in normal connection with the central structures excited.

In performing the experiment of exciting one hemisphere after ablation of the

other, it is clear that the association through the superior peduncle of the cerebellum affords a means whereby the opposite lobe of that organ might be aroused, and so produce the tonic contractions of the limb on the side of excitation. This view is suggested to us more especially by the teachings of Dr. HUGHLINGS JACKSON, and it obviously must be excluded before a positive opinion can be expressed as to the bilateral representation of the limbs in the excitable cortex of one hemisphere.

From none of the foregoing researches can it be determined to what extent the bulbo-spinal centres are associated with bilateral movements, since in all experiments in which muscular contractions are taken as an index their functional activity is included.

Having laid before the reader these general considerations by way of preface, we will proceed to describe our own experiments, as far as they suggest fresh evidence for or against the different views just enunciated.

#### EXPERIMENTAL RESULTS IN CONNECTION WITH BILATERALITY

The obvious elimination which the use of our method enables the experimenter to obtain is the removal of the influence of the bulbo-spinal centres.

This elimination is effected by the division of the spinal cord in the dorsal region, and the observation of the electrical changes occurring in its central end when the lower limb area of the cortex cerebri is excited. It is, however, essential to divide the descending tracts in the cord into two halves. This is done by splitting the cord longitudinally in its antero-posterior plane. The mode of operation employed has been described in Chapter III, Section 2,\* and the preparation shown in Plates 31 and 33.

\* It might reasonably be conceived that this operative procedure would seriously impair the conducting power of the cord. Although, as we point out in Chapter III, the posterior columns suffer somewhat, this is not the case with the lateral columns, the seat of the pyramidal tract to be investigated. An example of this is to be seen in the following case, where the effects in the divided cord of exciting but one hemisphere do not, when summed, fall far short of the effects obtained before the longitudinal section.

Cat (324)	Part excited	Duration of excitation	Coil	Part observed	Galvanometer reading	Muscular effect noted
Whole Cord divided and connected to galvanometer at 13th dorsal vertebra	Excitable area of left cortex	Secs 5	6,000	Whole cord	260	Slight fit
	" " "	"	8,000	" "	340	Fair fit
	" " "	"	10,000	" "	510	Powerful fit
Cord divided longitudinally and each half connected with galvanometer	" " "	"	6,000	{ Left half Right half	{ 50 220	{ Good fit
	" " "	"	8,000	{ Left half Right half	{ 45 195	
	" " "	"			210	" "



As regards the method of observation, the electrical changes in each half of the longitudinally divided cord were recorded by means of the galvanometer, since it was essential to obtain results which admitted of relatively strict comparison as to their amounts. Each half of the cord was therefore attached to an independent pair of non-polarisable electrodes, and an arrangement made by which either pair could at any desired moment be switched into connection with the wires leading to the galvanometer, &c.

The result of this experimental investigation may be divided into groups, each one of which we must consider in detail

I.—*Excitation of Cortex (whole Encephalon intact) —Electrical Changes in each half of Longitudinally Divided Cord.*

The cord having been divided, and split as just indicated, one cortical surface was exposed and the animal having been brought as far as possible into a perfectly steady, *i.e.*, constant state of narcotisation, the same strength of stimulus was then applied to the cortex, first one half of the cord being in connection with the galvanometer, and then the opposite half (see fig. 8). The results obtained, *i.e.*, from the opposite side of the spinal cord, and from the same side respectively, were then gathered together and averages taken

It will be best to begin with the results of special experiments. Of these, the first we will refer to were made upon an animal (Cat 237), in which, from the movements of the upper limb, it was very easy to ascertain when the muscular contractions were unilateral or bilateral. It was seen that when the said contractions were strictly unilateral, the excitation of the hemisphere produced *no result* in the half of the cord on the same side, but a marked result in the half of the cord of the opposite side, *viz* , 275 degrees of the scale.

In this case complete unilaterality for the lower limb existed as far as the pyramidal tracts in the cord were concerned, for the cortex was, as we have before indicated in the first of our considerations, completely discharged, the discharge being evidenced by the large effect in the corresponding half of the cord, yet no electrical change could be seen in the other half indicative of descending impulses

In another experiment made upon a Monkey (215), both cortices were exposed for excitation. In this animal, it was easy to confine the excitation apparently to one hemisphere, although, judging from the contractions of the muscles of the upper limb, the cortex excited was very completely discharged. In this instance, the cord was divided as described between the 10th and 11th dorsal nerves, the resting electrical difference of the two halves was in the proportion of two to one, the smaller being the right

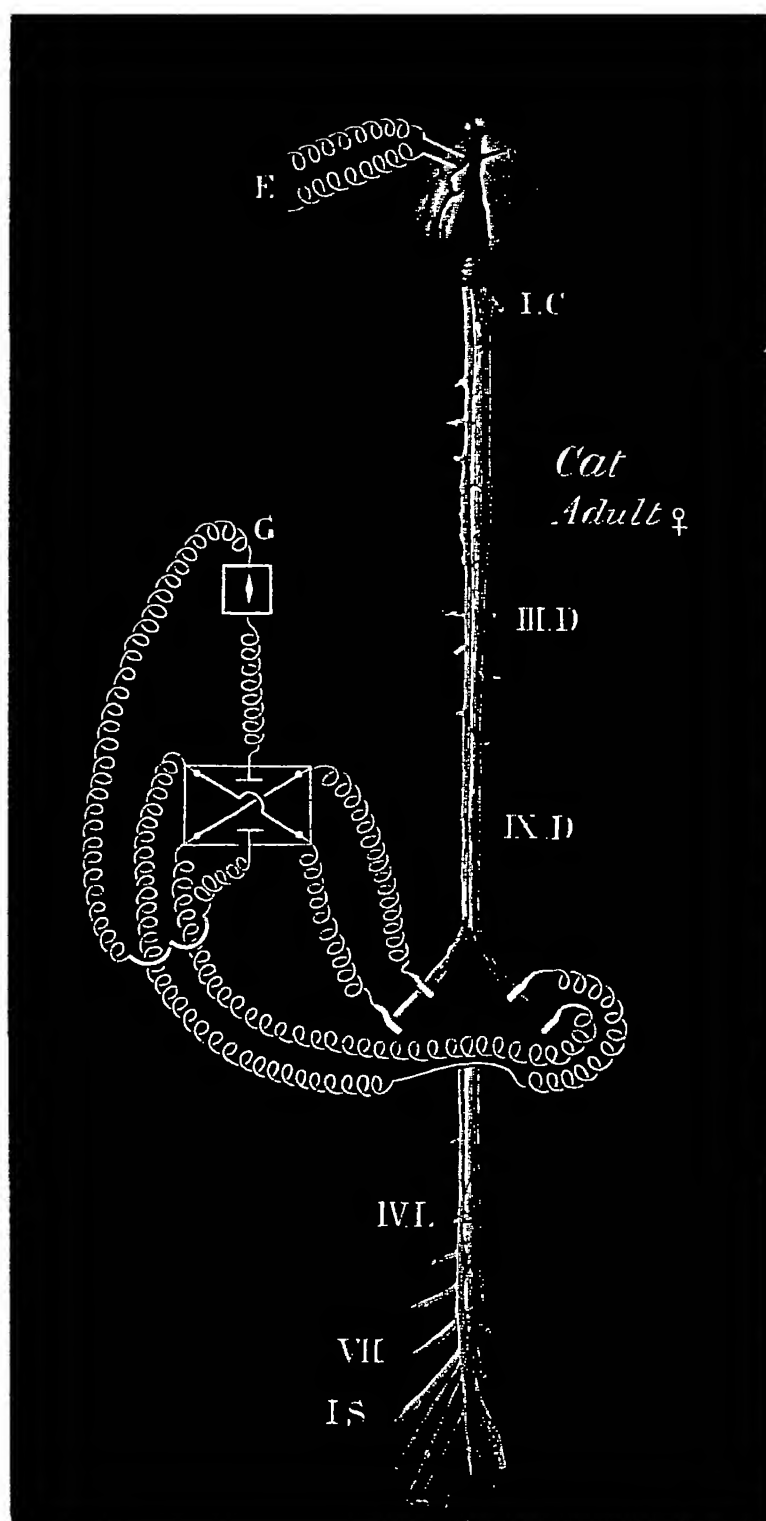
For the convenience of brevity, we will speak of the halves of the cord as the "right cord" and "left cord" respectively.

Excitation of the left hemisphere gave, with the coil at 5000, an effect in the right half of the cord of 425 degrees, and then, the right cord still remaining in connection



with the galvanometer, the right hemisphere was stimulated, the result being an effect of only 22 degrees. This last result, in addition to being only a twentieth of that evoked by the corresponding cortex was probably due to discharge from the left hemisphere, for, after the cortex had been allowed to rest, this pair of observations was

Fig 8



repeated with the following striking results, viz, the right cord being observed, the left hemisphere was excited, with a resulting variation of 365 degrees. The same cord being still led off, the right hemisphere was excited, i.e., the hemisphere of the same side, and *no effect* was produced in the galvanometer. The same degree of narcotisation being maintained, and the same strength of coil being employed as that

just mentioned, viz., 5000, the left cord was then connected with the galvanometer, excitation of the right hemisphere (i.e., that of the corresponding side) gave 375 degrees, and excitation of the left hemisphere (i.e., that of the same side) only gave 8 degrees. This mode of pairing the observations is clearly one likely to give the most useful results, but we also paired the observations in the following way, viz., by connecting first one side of the cord with the galvanometer and then the other, in each case stimulating the same hemisphere.

The foregoing two selected experiments illustrate the conditions which are observed with the hemispheres in a normal state. Before considering the further evidence afforded by massing our observations, we must draw attention to the greatest difficulty in connection with this branch of enquiry, and which prevents us from speaking so positively upon this point, when the results noted at the beginning of any experiment are added to those recorded at the end. We refer to the great tendency of the cortex to become hyperexcitable after one or two excitations, and, consequently, for the excitatory state to pass from one hemisphere across to the other.

This is especially liable to occur when through repeated excitation the cortex has been thrown into a hyperexcitable state. This is, in fact, the objection which may be urged against any conclusions derived from massing together results, many of which being repetitions involve previous excitation. The same objection can also be urged with equal truth against the results of most of the observations of earlier experimenters; but upon the question whether this objection accounts for the whole of the results to be immediately given, we have no means of expressing any decisive judgment. It is, however, easy to understand that a considerable proportion of the bilateral effect noted in the two halves of the cord when all the results are taken may be due to this circumstance.

The average amount of the bilateral effect obtained in the two halves of the split cord when one hemisphere is directly excited is as follows:—

	Cord.	
	Opposite half	Same half
Cat—Average of 12 observations	157	33
Monkey—Average of 31 observations	158	32

It will be seen that when all results are averaged together there is an effect on both sides of the cord, and that its amount in the half opposite to the excited cortex is five times as great as that in the half which is on the same side.

The close identity of the figures in the two animals is remarkable, and not what our early observations had led us to anticipate.\*

\*One of us (V. H.), however, had already shown by experiments with absinthe combined with

The method under consideration, with both cortices exposed but intact, is not, however, favourable for testing bilaterality, since we have often had occasion to observe the great inequality in the excitability of the two hemispheres, which appears to be to a large extent connected with the necessary exposure of one cortex before the other

From the result of other experiments we are inclined to believe that the effects (average 32) observed in the half of the cord on the side of the cortical excitation is due to the passage of impulses which have descended from the cortex opposite to that directly stimulated, but several interpretations are, of course, possible. In this connection it must be remembered that we do not yet know whether a *direct* pyramidal tract exists in the Carnivora (most authors denying its presence), and, further, that possibly even the galvanometer may not show an excitatory disturbance if the fibres by which the hemisphere of one side might be in relation with the same side of the spinal cord were very few in number.

## II *Excitation of Cortex—Effect in Cord after previous Hemisection*

The next step was to ascertain the effect of a previously performed hemisection of the cord between the encephalon and the observed region, the experiment being made with the view of eliminating any presumably crossed discharge from the cortex opposite to that excited

The following experiment was made. In a Cat (225) the right half of the cord was divided under antiseptic precautions at the level of the lower border of the 9th dorsal vertebra. In this case there was well-marked motor paralysis in the right hind limb with rigidity, and diminution of perception of sensory stimulation of the same limb. The right knee jerk was exaggerated. When partly etherised the right hind limb became flaccid and the left somewhat rigid, the knee jerk then on the right side was greatly exaggerated and marked clonus present. These facts were noted just before the experiment now to be described. Eighty-four days later the cord was exposed and divided below the lesion, and the central end of the whole cord connected with the galvanometer electrodes. (See fig 9.) The two cortices were then exposed and excited with an intensity of stimulus indicated by coil 8000 for 5 seconds.

The following definite results were obtained —

In the first place excitation of each hemisphere evidently produced unilateral epileptic fits. The effect in the descending (lower limb) fibres of the cord was as follows, it being remembered that the right half of the spinal cord had been divided. Excitation of the right cortex which produced unilateral fits on the left side of the body, gave a variation of 82 degrees in the galvanometer, whereas excitation of the left cortex, although it produced a good unilateral fit in the parts above the section, *i.e.*, right upper limb, gave nothing in the galvanometer, although the *whole* cord ablation of one hemisphere or excitable area in Cats, that apparently in that animal complete unilaterality of the true cortical discharge (*i.e.*, tonus *plus* clonus) existed

was the seat of galvanometric observation. In this way it was obvious that, when the excitation was so limited to one hemisphere as to produce only unilateral muscular movements, no impulses descended the fibres on the same side of the spinal cord

Fig 9



Note the hemisection of the cord on the right side at the level of the 9th dorsal vertebra.

and all impulses passed down the side opposite to that of the hemisphere excited.

That this conclusion was correct was confirmed by observing that even when on repeating the experiment a bilateral fit was obtained from stimulating either cortex,

whilst the cord effect evoked by the right cortex was increased to 134 scale, an effect was also evoked by excitation of the left cortex, though it amounted to only 15 scale

The cord was next divided longitudinally and the electrical change observed on the two sides with the following result, it being remembered that the right half of the cord had been interrupted by the previous hemisection

	Excitation	Left half	Right half
Left cortex	6000, 5 secs	trace	trace
Right ,	" "	50	
Left "	6500, "	trace	trace
Right "	" "	215	
Left "	8000, "	5, 6, 20	
Right "	" "	150	

It is clear from this that in the half of the cord (left) which offered an uninterrupted channel, the excitation of the cortex of the opposite side evoked large results, whilst the excitation of the cortex of the same side side evoked no results until a considerable intensity of stimulus was used and a bilateral fit produced. On microscopical investigation the lesion in the cord showed that the whole of the right half of the cord was destroyed, and the anterior third of the left posterior column, and the left posterior median. The descending degeneration, therefore, affected the right pyramidal tract in the lateral column only. The ascending degeneration affected both postero-median columns and the right cerebellar and antero-lateral tracts.

It should be mentioned that SCHIFF's observations on hemisections made just before excitation of the cortex show that the same relationships prevail as regards muscular movements.

### III *Excitation of Corona Radiata — Electrical effect observed in each Half of Split Cord*

The general electrical phenomena observed after excitation of the corona radiata, and especially as contrasted with those elicited by exciting the cortex are described in Chapter VI, but in attempting to still further elucidate the subject of bilaterality we arranged a third variety of experiment, originally designed for the graphic method by FRANCK and PITRES and others, viz., the investigation of the bilateral phenomenon noted after excision of the cortex, and consequent upon excitation of the subjacent corona radiata.

We have considered, on p. 338, the errors it involves, and have always endeavoured to minimise them as far as possible just as in the case of the cortex. Although the results are thus of necessity only to be accepted with reservations on the points already mentioned, which we must again briefly notice, nevertheless they do afford some very suggestive deductions.

We will first give the results obtained in the longitudinally divided cord by excitation of one corona radiata

In this series of experiments we connected either half of the longitudinally divided cord with the galvanometer as in the cortex experiments previously described

We have not yet seen any absolutely unilateral effect, as in the case of stimulation of the cortex. Very often the effect in the same side of the cord was extremely small (once only a trace), *e.g.*,  $4^{\circ}$ ,  $6^{\circ}$ ,  $8^{\circ}$ , &c, but it was always present. On massing the results together, *i.e.*, adding the observations in the Monkey to those in the Cat, we obtained the following proportionate averages:—

Half of cord on same side as excitation of corona— $14^{\circ}$  mean of 12 observations.

Half of cord opposite or corresponding to the corona excited— $50^{\circ}$  mean of 13 observations

The proportion, therefore, is 7 to 2, whereas the cortex proportion is almost 5 to 1, and often purely unilateral. Consequently it appears that bilateral phenomena are more easily elicited by exciting the corona radiata than the cortex cerebri, provided the same care is employed to avoid as far as possible in both cases errors due to spread, &c

The explanation of this is not far to seek, and, if correct, throws more light on bilaterality. It simply consists in the obvious fact that removal of the cortex lays bare a crowd of association fibres, the excitability of which is heightened by the section removing the cortex, and that it is the spread of the excitatory effect along these fibres to other central mechanisms in the encephalon, *i.e.*, opposite cortex, cerebellum, &c., which produces the bilateral phenomenon. It is thus extremely likely that bilateral tonus should occur after stimulation of but one corona radiata.

In accordance with what we have said before respecting the influence of ether, this reagent afforded an opportunity of testing the truth of the foregoing views, since the influence of bilateral central mechanisms could be by this means in part excluded, and it could therefore be seen whether or no there was a corresponding modification in the bilateral character of the effect.

We found that deeper etherisation invariably tended to restore in a great measure the inequality between the two cord effects, the difference between the two being much greater in proportion as the degree of anaesthesia increased. This again seems to indicate that any markedly bilateral effect is due to an additional functional activity in the cortex on the opposite side to the excited corona.

#### IV. *Excitation of Corona Radiata.—Effect in Cord with previous Hemisection.*

It was necessary now to repeat the design of the graphic experiments as employed by FRANK, SCHIFF, LEWASCHEW, and others, using, however, our present electrical method, that is to say, observing how far a hemisection of the cord between the

encephalon and the part observed interrupted the propagation of impulses from the corresponding corona fibres.

The hemisection was made in the case (Cat 225) before referred to, p 356, two months beforehand, at the 9th dorsal vertebra. For the observation the cord was exposed, divided, and split longitudinally at the level of the 1st lumbar vertebra. Both coronæ radiatæ were then exposed and excited alternately, the effects evoked being given below.

Excitation	Cord	
	Galvanometric effects	
	Left half	Right half.
Right Corona, 12,000, 3 seconds	30	0
Left       "       "       "	Trace	0
Right       "       13,000,       "	51	
Left       "       "       "	4	

In this case it is evident that the effect was almost completely unilateral.

In another case in which the hemisection was made at the time, there was no complete unilateral effect, but excitation of both coronæ elicited changes, the corresponding corona evoking an effect which was twice as large as that produced by stimulation of the one on the opposite side to the lesion. By means of etherisation the proportion was increased to 3 to 1, but since the alterations in excitability, due to the lesion being performed at the time, were disturbing factors, the influence of which could not be gauged, the experiment was not pursued further. It may be fairly concluded, however, that the more perfect the elimination of such complications, the more complete is the unilaterality of representation.

#### V *Excitation of Corona Radiata after Complete Removal of one Hemisphere — Effect in each Half of Divided Cord.*

In order to endeavour to ascertain whether the bilateral effect was in relation, not merely with the discharge of portions of the cortex of the hemisphere opposite to that of the excited corona, but also in relation with the basal ganglia and the cerebellum, we have in one animal (Cat 309) observed the influence of complete removal of one cerebral hemisphere.

The cord was, in this case, split longitudinally, and both coronæ exposed for alternate excitation, the results of several observations being given below.



Excitation of one corona	Effect in opposite half of cord	Effect in same half
Right, 8000, 5 seconds	160	20
" " "	61	8
" " "	52	20
Left " "	54	34
" " "	54	11
" " "	50	25
	6 = 431	6 = 118
Average	72	20

The left cerebral hemisphere was now removed, and the effect of excitation of the right corona observed in each half of the cord

	Opposite side.	Same side
Right corona	100	27
	75	30
	2 = 175	2 = 57
Average	87	28

The result is to show that the bilaterality continues, and apparently to the same extent as before.

The experiment is one which needs careful repetition, and special precautions to prevent errors.

#### VI. *Excitation of Cortex and Corona Radiata.—Effect in Sciatic Nerves.*

It has been already stated (Chapter V, Section 2, p 332) that the excitation of the cortex evokes electrical effects in the sciatic nerves, and, further (Chapter VI, Section 2, p. 339), that similar effects are evoked by excitation of the corona radiata. A comparison between the amounts evoked in the nerves by excitation of one cortex, or by observation of the changes in one nerve consequent upon alternate excitation of each hemisphere, throws additional light upon the question of bilaterality of representation of the limbs now under discussion. It will be in the remembrance of the reader that the nerve effects derived from cortical excitation are remarkably small in

amount, in consequence of this, the comparison necessarily becomes less exact when the method of averages is used.

The following table gives this comparison in the case of six animals, four Cats and two Monkeys. In three cases, (a), (b), (c), the effect was observed in one nerve and each cortex alternately excited, in the remaining three cases, (d), (e), (f), the observations were made upon each nerve, one cortex only being exposed and stimulated.

	Intensity of stimulation	Effect in nerve of opposite side	Effect in nerve of same side
(a) Cat (296)	11,000	5 9 12 20	0 0 0 0
(b) Cat (290)	12,000	18 10 22	2 0 0
(c) Cat (298)	12,500	28	0
(d) Cat (299)	12,000	12 20 10	10 0 0
(e) Monkey (54)	5,000	16 18	5 1
(f) Monkey (217)	5,000	18 28 16	0 18 5
		262	41
Average		16	2.5

From this table it is seen that, in the large majority of cases, unilaterality strictly prevailed. The small average amount of the bilateral effects, dependent, moreover, as it is upon a very few high readings, suggests that these results are due to that constant source of error in experiments upon bilaterality of representation, viz, hyperexcitability in other parts of the encephalon, produced by the operative procedure.

Examination of our records shows that when one corona is excited, and first one nerve and then the other connected with the galvanometer, the following average results were obtained —

Corona radiata excited.

Average of all effects      Nerve opposite side 26 (23 observations).  
Nerve same side 11 (20 observations)

This average, however, is the result of all the observations made, some of them being markedly bilateral in character. There are, however, no less than six cases in which no effect at all was observed on the same side as the excited corona,

and four cases in which the effect was under 10, and averaged only 4. It is, therefore, only by including cases of bilateral effects produced by powerful tonic discharges that the above total average is so comparatively high

If, therefore, these higher figures were separated from the Table, we should find that the average effect on the same side would be not more than one-sixth of that on the opposite side, whilst, with evident and powerful bilateral discharges, the former effect amounts to one-half of the latter

### *Summary of Facts*

The facts brought forward in the preceding pages seem to show that it is possible to obtain completely unilateral effects in both spinal cord and nerve when one cerebral hemisphere is excited, but that an increase in the intensity of the stimulus, and a diminution in the degree of narcosis, favour the production of bilateral effects—the inequality between the crossed and uncrossed effect becoming less and less marked in proportion as these favouring circumstances are augmented.

The conclusion to which the previous observations seemed to tend, that in one cortex bilateral representation of the limbs exists, does not seem to be supported by the present experiments, since such bilateral effects as may be witnessed are specially brought out by agencies which may be supposed to bring into play other portions of the central nervous system, particularly the opposite excitable cortex, the cerebellum, and basal structures. We feel, however, that without definitely proving this, our experiments have the result of making the question of bilateral representation in one cortex an open one, at least for the Carnivora

To this position all we wish to add is our view that the weight of evidence goes to show that, where the excitation is properly limited to the cortico-pyramidal system, unilaterality of representation of the lower limb muscles appears to exist.

How far this is correct only further researches by the electrical method will, we believe, be successful in showing, and we hope that others will forward the investigation of this point

## CHAPTER VIII—ON THE ELECTRICAL EFFECTS EVOKED IN THE SPINAL CORD BY THE EXCITATION OF THE VARIOUS PARTS OF THE SAME

- Section 1 —Introductory
- Section 2 —Propagation of Impulses by the fibres of the Cord
- Section 3 —General characters of electrical effects in the Cord following its excitation
- Section 4 —Excitatory electrical effects in the Cord, as evidenced by the Electrometer
- Section 5 —Electrical effects evoked by localised stimulation of the Spinal Cord, plan of experiments
- Section 6 —Electrical effects in the Lumbar Cord, following excitation of the Dorsal Cord
- Section 7 —Electrical effects in the Dorsal Cord, following excitation of the Lumbar Cord
- Section 8 —Electrical effects in each half of the divided Cord
- Section 9 —Influence upon electrical effects in the Cord of intervening sections of the various columns.
- Section 10 —Summary of results of experiments

## SECTION 1 —INTRODUCTORY

The electrical changes produced in the cord by excitation of the cortex, and of the fibres of the corona radiata, whilst due to the passage of nerve impulses along tracts in the spinal cord, derive their interest from the further knowledge which they give us with reference to the functions of the excited parts in the encephalon from which those impulses spring

It is otherwise with the material of this and the succeeding chapters, since the electrical changes, now to be described, are evoked by the excitation either of the different parts of the cord itself, or its nerves. The method of determining the characters of the functional activity of nerve tissue, by the study of those electrical effects which undoubtedly accompany and indicate the extent of that activity, is thus to be now applied solely with relation to the cord.

Since the functions of the cord are naturally divisible into those connected especially with its fibres—conductivity—and those connected especially with the activity of its cells, of which reflex action is the example, the present method was applied in any given experiment with special reference to the elucidation of one of these two branches of enquiry, it being always borne in mind that, as a matter of fact, the two groups of function overlap.

The question of the localisation of paths, in the fibres of the cord alone, has at present been only approached in reality by the method of histological experiment, including the embryological and degeneration methods, since previous physiological observation, relying on movement as an index, has always included the whole of the neuro-muscular mechanism

The sole method for obtaining actual indications of the conduction of physiological processes in the fibres of the cord, is that of determining the presence in them of excitatory electrical changes. We have, therefore, carried out a very large number of

experiments upon the spinal cord under very different conditions, with the express purpose before us of obtaining data which should give clear evidence of the conduction of nerve impulses in its fibres and centres respectively. The results furnished by our experiments may be split up into the following groups —

A The experimental evidence of definite localisation of the channels of conduction of nerve impulses afforded by electrical changes in the cord, when evoked by stimulation of its different parts, whether distal or proximal

B The evidence of the localisation in the cord of fibres which enter it by the roots afforded by electrical changes in the cord when evoked by stimulation of its nerves

C The evidence of the relations of the spinal cord to the nerves afforded by electrical changes in the nerves, when evoked by stimulation of separate parts of the cord

D The experiments elucidating the complicated group of phenomena in relation with the reflex activity and function of the spinal nerve cells. This may be expressed as follows —

The evidence afforded by the electrical changes, in both cord and nerve, of the nature of the rôle of the nerve corpuscles in the cord

To obtain a sufficient mass of evidence, to establish even a few conclusions in these four subjects, a large number of experiments have been carried out, constituting by far the larger share of the work we have done since our preliminary communication in the 'Proceedings of the Royal Society,' in 1888

The groups of data just indicated, in which these results are expressed, will be treated of in the succeeding four consecutive chapters, group A. in the present Chapter VIII, B in Chapter IX., C in Chapter X., and D. in Chapter XI, this being the order which seems to us at once the most natural and the most likely to present the conclusions in a logical and thus intelligible manner.

We therefore now pass to the consideration of the experiments, confining ourselves in this chapter to the electrical changes evoked in the spinal cord by stimulation of its different parts, and these only.

It is, however, first necessary to say a few words on the general question of conduction in the nerve fibres of the cord

## SECTION 2 — PROPAGATION OF IMPULSES BY THE FIBRES OF THE CORD.

It has been maintained that the nerve fibres of the spinal cord do not respond to direct stimulation, in the same way that the fibres in a mixed nerve do,\* and that it is the cellular elements alone which respond to excitation, the resultant nerve impulses being therefore, according to this view, indirect. The experiments to be detailed in this and the succeeding chapters will give convincing proof, if that is necessary, of the

\* VAN DIEN, 'Nederl. Tijdschr. v Geneesk,' vol. 3, p. 393. MOLESCHOTT, 'Unters z Naturl.' 1860  
 11. 7, p. 380

erroneous character of this view. The nerve fibres in the cord respond to direct excitation, like those in the nerve roots and nerve trunk, that is to say, nerve impulses, with their accompanying electrical effects, are propagated in both directions along any *continuous* nerve fibres which may exist in the excited area, but, in addition, complications are introduced by the connection of a large number of the fibres with nerve cells, this connection causing now a possible decrease in the total electrical effects, presumably by the blocking of the path and the falling out of certain impulses, now an increase, presumably by the awakening of cells which lie in the path, and the accession of fresh impulses generated in these structures.

We will first state in general terms upon what facts rests our present knowledge of the mode of propagation of nerve impulses, from an excited area of the cord along continuous paths to a distant unexcited area.

(a) It has been already pointed out in the historical introduction that the methods of histological investigation, particularly those associated with the presence of developmental and degenerative changes, have unravelled from the skein of nerve fibres in the cord certain tracts, and grouped them into columns of a continuous character in the lateral and posterior regions respectively. The limits of our knowledge have already been alluded to, but the inadequate character of the method is shown by the large number of fibres which are displayed in each transverse section of the cord, and the comparatively small number as to which a continuous connection with other parts of the cord has been demonstrated.

(b) When we turn to the results of physiological experiments, the only method which has furnished satisfactory indications of direct physiological continuity in a tract of nerve fibres is that employed by WOROSCHILOFF, SCHIFF, and others, of exciting the peripheral end of the cut cord below the medulla and observing the muscular movements of the lower limbs, in one case with the lower part of the cord intact, in another with a section of some structurally known column. In this way it has been shown that a group of fibres in the lateral column forms a path of such direct continuity between the seat of excitation in the cervical region and the lumbar cord that its section interrupts the passage of the descending nerve impulses generated in the former region, and it is therefore inferred that this path is, physiologically speaking, directly continuous.

(c) Another method of determining the character of propagation in the spinal paths is the classical method employed by HELMHOLTZ in the case of the nerve trunks, that is, the measurement of the transmission time. This, in the case of the fibres in the nerve trunk (Frog, Rabbit), is generally held to be about 33 metres per second, though in Man the conduction along sensory fibres is stated to be twice as fast. The experimental determination of this latter is, however, complicated by the methods used, which include the measurement of the individual reaction time, and introduce, therefore, additional uncertain factors which blur the clearness of the results.

Similar attempts have been made to determine the rate of conduction of nerve impulses in the spinal cord, both centrifugal and centripetal in character. Most of the experiments have been made upon Man by measuring the reaction time, and are therefore more or less untrustworthy owing to the conditions just mentioned. EXNER\* obtained thus a mean result for centrifugal impulses of 11 to 12 metres in 1 second, for centripetal impulses of 8 metres. On the other hand, VON WITTICH,† by the use of a similar method, had previously obtained a rate of 26 metres for the centrifugal impulses. We have been unable to find any description of observations upon the Cat with regard to conduction, though such might easily be carried out by the use of the graphic method, and since it was important for us to know the behaviour of the fibres in the cord in this respect, we devoted a few preliminary experiments to the determination of conduction time only.

These experiments may be briefly described as follows:—

The cord was exposed in the anæsthetised animal in the lower cervical and lower dorsal regions respectively; the rectus femoris muscle was then selected for graphic record. The advantages offered by this muscle are—

- (1) Its anatomical relation with the pelvis, enabling the leg and trunk to be fixed, and the muscle brought out at right angles to the body.
- (2) The ease with which it could be separated from the surrounding parts
- (3.) Its own structure—that of a long thin muscle, with parallel fibres

The lower tendon of the muscle was divided and ligatured; the ligature was then attached by means of a pulley to the lever of TIGERSTEDT'S break key,‡ so adjusted that the smallest contraction of the muscle was sufficient to raise the lever, and thus break an electrical contact. This contact formed part of an independent circuit, including one of SMITH'S new chronographs§ and three storage cells, it was ascertained that the movements of the chronograph armature occurred within  $3/10000$  second of the break of the circuit.

The movement of the chronograph lever recorded upon the travelling glass plate of a spring myograph (*Federmiographion*), the rate of movement being 25 centims in  $1/100$  sec. The lateral column of the exposed cord was excited by a single induction shock, which was obtained by allowing the traveller to break, at a given point of its course, the primary circuit of a KRONECKER'S inductorium. As the moment of break was always the same, the break induction shock obtained was uniform in all cases, both as to intensity and time of occurrence, the position of the secondary coil was 2000.

The following measurements were obtained of the duration of the period between

\* EXNER, PFLÜGER'S 'Archiv,' 1873, vol 7, p 632

† v WITTICH, 'Archiv f. Pathol Anat,' 1869, vol. 46, p 476

‡ *Loc cit*

§ *Loc. cit*



excitation and commencement of muscular response, when the former occurred at the level of the 5th cervical and 2nd lumbar nerves respectively —

## CAT (163)

Excitation at 5th cervical	Excitation at 2nd lumbar	Difference
0217	0170	0047
0210	0170	0040
0217	0172	0045
0241	0200	0041
Average 0221	0178	0043

The distance between the 5th cervical and the 2nd lumbar was found to be 17 centims, and since the average difference of time between the muscular response evoked by the excitation at the two regions is 0043, this difference indicates that the cord delay is such as would be caused if the nerve impulses starting from the cervical region travelled along the cord at  $39\frac{1}{2}$  metres per second. This experiment, therefore, seems to show that the time occupied by the conduction of nerve impulses in the Mammalian cord closely resembles that occupied by their conduction in nerve trunks; and it confirms the view that there is an efferent path in the cord leading from the cervical to the lumbar region in which a physiological continuity exists similar to that which forms the basis of nerve conduction in the fibres of mixed nerve trunks.

It will be noticed that the more exact physiological methods just referred to rely upon the observation of muscular movements. This involves serious disadvantages, since, in the first place, the method is thereby limited to the efferent fibres, and thus the physiological scope of any inquiry is narrowed; whilst, in the second place, the structural connections between the efferent fibres in the cord and the anterior roots of the nerves is to a great extent unknown, and certainly involves cellular elements, thus introducing new physiological conditions.

There is, as it seems to us, only one line of experimental enquiry which is free from these objections—that, namely, of ascertaining the existence of the nerve impulses in the fibres of the spinal cord itself, through careful quantitative observations of the electrical effects by which they are accompanied.

The present chapter will be devoted to the consideration in detail of the results of such observations in the dorsal and lumbar regions of the cord respectively. The novelty of the method, and the important bearing which the results have upon the physiology of the cord, we trust will warrant this extended treatment.

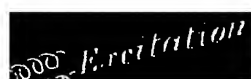
## SECTION 3 —GENERAL CHARACTER OF THE ELECTRICAL EFFECTS IN THE CORD

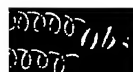
The earliest experiments we made upon the cord showed that pronounced electrical changes always occurred in any portion of the lower dorsal and lumbar regions when some other portion in continuity was excited electrically. The simplest method of


Fig 10


 I.C.


 Adult


 Excitation


 Obs.


 V.L.


 VII

excitation was that of inserting needles into the cord, the needles being connected with wires attached to the secondary circuit of the inductorium. It is obvious that if the excitation was carried out upon the cord whilst still in connection with the cerebrum, any resultant effects in the former would be the sum of the direct excitatory

changes and those indirectly produced by the reflex discharge of the cortex, as described in the preceding chapters. To avoid this and to obtain uncomplicated effects the cord was always severed from its connection with the higher centres.

The plan followed in the experiment was, therefore, as follows: two situations were selected, in almost all cases about the level of the 8th dorsal and 2nd to 3rd lumbar vertebræ, the cord was then first exposed for a short distance at the upper one and divided. It was then carefully exposed in the lower region and divided again, the upper division being made first in order to diminish, by cutting off all connection with the higher centres, the shock which subsequent operations necessarily involved. The portion of cord (see fig 10), included between the upper or 8th dorsal section and the lower or 2nd lumbar one, formed thus an isolated fragment, and since it was upon this portion that the experiments to be detailed were carried out, this fragment may be termed the "experimental region" of the cord. A portion of this experimental region was always prepared for observation at either its dorsal or lumbar end, the preparation consisting in the exposure of from 4 to 5 centims of the cord in immediate connection with the cross section and the division of all root and other attachments. The cut end of the portion was then ligatured, and the prepared part raised from the canal and suspended in air, care being taken to avoid all undue pull upon the structure. As previously described, (see Plate 29) the trunk was immovably fixed by holding the vertebræ in the ivory jaws of a clamp, which was rigidly attached to a metal rod fixed into the experimental table.

The ligatured end of the cord thus freed was attached by the before-mentioned cables of thread soaked in 6 per cent NaCl solution and plastered with kaolin, to the galvanometric non-polarisable electrodes, one cable being tied round the ligatured end and cross section, the other round the longitudinal surface about 1 centim. distant.

The usual resting difference between the surface and cross section was found to be present in all cases, and was always kept carefully compensated, its characteristics have been fully gone into in Chapter IV., and it will therefore not be further alluded to here.

If the other exposed end of the experimental tract were now excited, either by thrusting through it a pair of needle electrodes, or by placing upon the cut end the points of a pair of ordinary platinum electrodes, an excitatory electrical effect was seen in the portion connected with the galvanometric electrodes. This effect is always of such a character as to be opposed to the resting difference; it is suddenly developed with the commencement of the stimulation, and subsides on its cessation, being followed by the rise in the resting difference which is described in Chapter IV. It is evidenced both in the galvanometer and the capillary electrometer, the amount of deflection of the needle and of movement of the mercury being dependent upon (1) the nature, intensity, and number of the successive stimuli, (2) the condition of the animal.

(1) *Relation of the Effect to the Stimulus*A *Nature of Stimulus.*

(a) *Single Induction Shock*.—The effect can be evoked by a single stimulus, but in that case gives only slight deflections in the galvanometer, but appreciable movements in the electrometer. Thus, in one experiment (Cat 122) in which the dorsal end of the experimental tract was connected with the non-polarisable electrodes and the lumbar end with needle electrodes, on excitation by a single break induction shock the electrometer showed a sudden transient movement of the mercurial meniscus of considerable size, seven divisions of the eyepiece scale, with the single make shock, a movement of five divisions was observed, both movements being opposed in direction to that produced by the resting difference.

(b) *Repeated Induction Shocks*.—When the cord is excited by a rapid succession of equal and alternately directed induction shocks, more pronounced electrical changes are produced in the cord; the amount of the galvanometric change becomes very appreciable, amounting in some cases to two or three hundred scale, the amount of the effect in both the galvanometer and the electrometer varying with the intensity and direction of the successive stimuli. The best general idea of this effect is obtained with the latter instrument. The mercury is seen to leap at the moment of excitation in a direction opposed to that of the movement previously due to the uncompensated resting difference, this sudden change of level amounting to from 10 to 15 divisions of the eyepiece, it then slowly continues to rise until the successive stimuli cease, when a rapid subsidence to rather below its original level occurs.

(c.) *Mechanical Stimulus* —If with one end of the experimental tract in connection with the electrodes the other end receive a sudden mechanical stimulus, an electrical effect is evidenced in both galvanometer and electrometer. The most effective mechanical stimulus is that of sudden complete division or squeezing of the end of the cord; for this purpose ivory scissors were first used, but we afterwards found that if insulating precautions were taken, sharp metal scissors could be employed with more advantage, since the keenness of the blades ensured a clean cut and avoided the dangers due to dragging on the cord. Such a division produces a small deflection of 20 to 30 scale in the galvanometer, and a pronounced movement of from 5 to 7 (eyepiece divisions) of the mercurial meniscus.

After injection of strychnia, the slightest mechanical irritation of the cord or sensory impression evokes marked electrical effects in the galvanometer and electrometer.

B. *Intensity and Number of Stimuli.*

Other things being equal, the cord electrical effect varies directly with the intensity and number of the successive stimuli, a limit being reached in this respect, the change

being conditioned in the same general way as is the well-known electrical effect in the excited Frog's nerve.

As far as the galvanometer is concerned, since the falling time of our instrument was 10 seconds, the effect for successive stimuli kept up for less than 10 seconds must be obviously directly proportional to the time, hence, in all exact experiments involving this instrument, it was essential that the duration of the period of stimulation and the number, therefore, of the successive stimuli used should be the same. This was effected by the revolving paraffin key described in Chapter III, which ensured a strictly uniform period.

## (2) *Condition of the Animal*

### A. *Anæsthesia.*

The character of the effect in the cord, unlike that in the nerve, is varied not only by the intensity of the stimulus, but also by the introduction of changes in the condition of the animal. These are connected with the awakening of the central cellular elements of the cord through the intensity of the stimulation used. The condition of the animal largely affects the limit of intensity at which any stimulus becomes adequate to arouse these corpuscular elements. Thus if profoundly anæsthetised a strong stimulus is necessary, but if the narcosis be but slight, a weak stimulus may evoke the result.

Although the subject of anæsthesia has been already referred to in Chapter III., it has such an important bearing on the present results that it must be reintroduced at this juncture. Our experiments abound with instances of the following character. In a Cat (371) the lower (lumbar) end of the experimental tract was connected with the galvanometer, and the lateral region of the cord in the upper dorsal section was excited with a series of 500 successive equal and opposite induction shocks (100 a second for 5 seconds). The galvanometric effect obtained was a deflection of 230 scale, the anæsthesia though complete as regards consciousness being of a comparatively slight character. The ether was now pushed and the anæsthesia made more profound, abolishing reflex movements, when the effect of a precisely similar excitation was indicated by 142.

In another animal (Cat 375) electrical effects similarly produced in a state of profound and slight anæsthesia show, when compared, the same differences, both with minimal and maximal intensities of stimulus.

	Profound anæsthesia	Slight anæsthesia
Cat (375)		
(Stimulus 500 minimal)	60 galvanometric scale degrees	190
	82 " " "	140
	98 " " "	215
(Stimulus 1000 maximal)	192 " " "	243
	273 " " "	295
	165 " " "	210
	295 " " "	410

Thus the degree of anæsthesia in which the animal happens to be influences the result very considerably, and is a convincing proof of the true physiological basis of the cord electrical effect, viz, that it is dependent upon the number and intensity of excitatory impulses in the observed region. It may be pointed out once more that this influence of anæsthesia is also sufficient to show, what might perhaps be otherwise suspected, that there is no objection to the use of the electrical method of stimulation through its possibly involving errors due to electrical escape.

Further proof that with the method of isolation used no such escape occurs is shown by the similarly directed effect evoked by both the make and break induction shocks, and by the production of the effect by mechanical stimulation. A still more convincing proof is, however, the complete disappearance of the effect on systemic death (See Chapter III., section 4.)

### B *Systemic death and injury*

The influence of systemic death upon the physiological condition of the spinal cord has been already referred to in connection with the resting difference. It was there stated that the difference keeps up and increases in the exposed portion of cord as long as it is in connection with a part which through the maintenance of an unimpaired circulation retains its normal state of nutrition. When systemic death occurs the difference immediately begins to fall, and in a very few minutes (2-5) the excitatory electrical effect disappears, the loss of excitability occurring in the case of the spinal cord with much greater rapidity than in the case of the sciatic nerve.

This disappearance occurs without systemic death if by any movement of the animal the cord is pulled upon, or if it is bruised in preparation at a point intervening between the seat of excitation and that of observation. Finally, the functional endurance of the tissue is dependent upon the animal used, differing in different species and in the different animals of the same species.

The most important general conditions by which the cord electrical effect is controlled, having been thus set forth, we pass on to consider what information a detailed examination of the characters and amounts of the electrical effects evoked under different circumstances, furnishes as to the structure and functions of the spinal cord.

In our earlier experiments we made use of the capillary electrometer, and we will, therefore, first briefly describe those made with this instrument.

#### SECTION 4 —EXCITATORY ELECTRICAL EFFECTS IN THE CORD INVESTIGATED BY MEANS OF THE CAPILLARY ELECTROMETER

The electrometer, owing to the rapidity with which the mercury moves, furnishes valuable information as to the alterations in character and amount of electrical changes which follow one another in rapid succession. We have already indicated the experimental advantages which this confers in the examination of the cord effects evoked by cortical stimulation\*. Since, however, the conditions which increase the sensitive characters of the instrument are to a great extent those which diminish its rapidity, it is almost impossible at present to obtain an instrument of sufficient sensibility for our purpose, without so slowing its movement that it takes more than  $\frac{1}{15}$  second for the mercury to complete its rise or fall. If, therefore, a series of transient electrical changes similar in direction, following one another at intervals of less than  $\frac{1}{15}$  second and all of equal intensity, are allowed to affect the instrument, then since the movement of the meniscus due to the first change would take  $\frac{1}{15}$  second for its completion, the second change will occur when the mercury is either in movement or has just completed its excursion and not returned; a second movement is thus super-imposed on the first, so a third on the second, until a limit of fusion is reached, this being dependent upon the fact that with each additional displacement the counter-pull of the surface tension increases, and finally the displaced mercury is maintained at a new level without any additional displacement perceptible on either side of the level attained. It is probable that an extremely fine vibration synchronous with the rate of successive electrical effects exists, but when the successive electromotive changes are uniform in amount, direction, and time relations, such a vibration must be extremely small.

A very different condition is introduced when these electrical changes are alternate in direction, since now each displacement by one effect, whilst still in progress, is counteracted by another in the reverse direction due to the succeeding change being of opposite sign to its predecessor. The effect of such a series of electrical changes even when following one another at such short intervals as  $\frac{1}{100}$  second is thus clearly visible, whatever level the mercury may have reached, as a blurring of the edge of the meniscus. The appearance to the eye may be described as a grey border to the otherwise black opaque column when viewed under the microscope.

This peculiarity of the electrometer at once enables us to judge whether, in a series of brief electrical changes, these are similar or dissimilar in direction, and we will first draw attention to this point in connection with the electrical effects in the spinal cord.

\* See this paper, p 324, also 'Roy Soc Proc,' Nov, 1888 (vol 45, p 18)



The present series of experiments being planned for purposes of quantitative measurement, the least complicated and most constant conditions were in all cases selected, these being associated with careful isolation, and with the presence of one electrode only in contact with the natural surface. It is probable that with these conditions the total excitatory electrical change in the electrode circuit is chiefly that produced by alterations affecting this one electrode.

We will now proceed to describe the character of the movements of the mercury when, with the capillary electrometer connected by the electrodes with an isolated portion of cord, this structure is stimulated by a series of induction shocks alternate in direction and following one another at intervals of  $\frac{1}{100}$  second (Helmholtz side-wire inductorium).

It has already been stated that one end of the "experimental tract" is prepared for connection with the non-polarisable electrodes, the other for excitation, so far as the character of the effect revealed by the electrometer is concerned, it makes no appreciable difference which end is respectively used for the purpose. In both cases a minimal excitation evokes an electrical change in the other end of the tract which affects the mercury of the electrometer, so that it moves rapidly up to a certain point, and there remains steady without visible oscillation, while it falls on the cessation of the stimulus, the mercury rapidly returning to its previous resting position.

With more intense stimuli a larger excursion of the mercury is obtained, and although no evidence of rapid vibration is detected, the character of the movement often becomes irregular, rising and falling at intervals in a more or less abrupt manner.

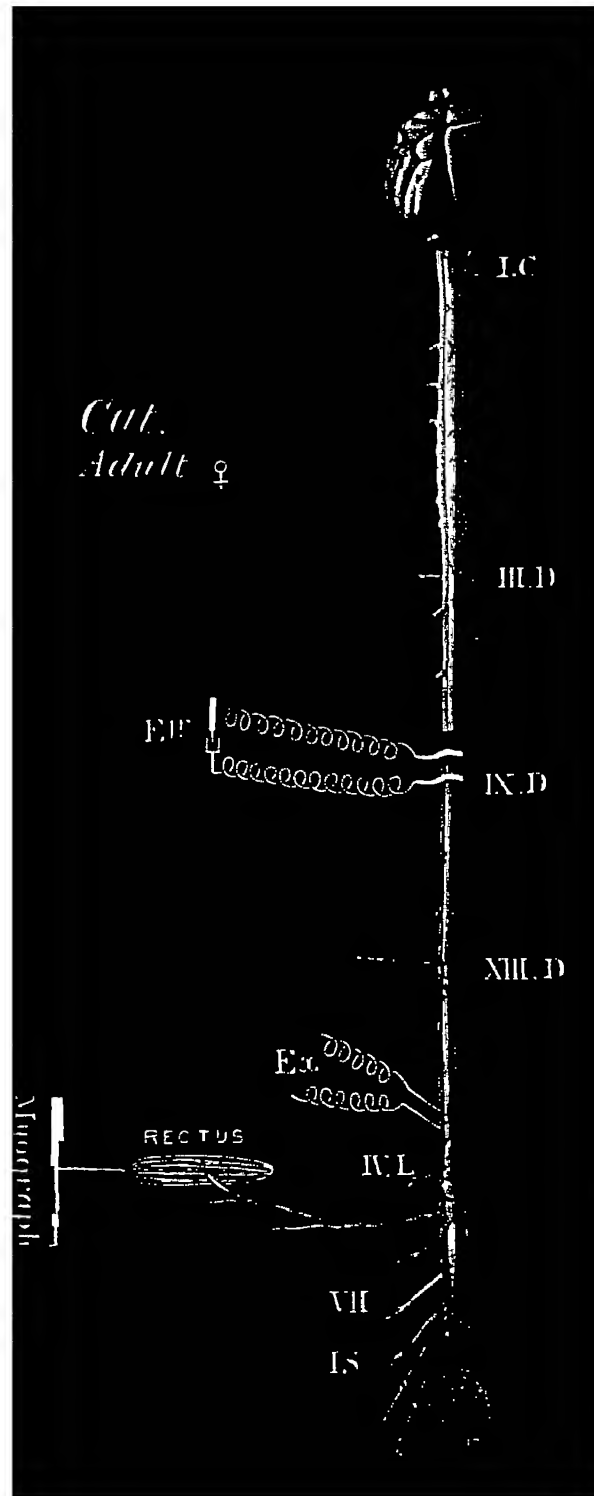
Whilst then it was clear from its character that the movement of the mercury is in no way connected with any electrotonic or other escape from the exciting circuit, since there is no evidence of rapid rhythmical alternating effect, synchronous with the number of stimuli, it was desirable to ascertain to what extent the irregularities just referred to were true indications of changes in the cord.

To ascertain this, experiments were made in which (see fig. 11) the cord was divided at one point only, the 8th dorsal, and the upper end of the lower fragment connected with the electrometer. The rectus femoris muscle was then prepared as indicated in the preceding paragraphs dealing with the transmission time (p. 366), but the attached ligature was fixed to a strong spring (FICK'S isometric myograph), the movements of which, as recorded by a lever, were magnified 50 times. The cord was then exposed in the lumbar region and its lateral surface excited, the muscular contractions were observed and recorded, and at the same time the character of any displacement of the mercury of the electrometer was ascertained as far as possible by the eye, and roughly drawn upon paper.

It was thus ascertained that the electrical effects in the dorsal region of the cord evoked by lumbar excitation, and evidenced by the mercurial movements, coincided in plan and character with the muscular effects.

Since the electrical changes evoked by excitation of the cord thus appeared to afford true indications of the passage of nerve impulses along its nerve fibres, it seemed to us quite possible to obtain for any one set of fibres a measurement of the value of the electrical effects in it which would bear comparison with a similar measurement

Fig 11



obtained in the case of some other set. By piecing together the information thus obtained, and by varying the conditions in which the cord was placed, we hoped to determine the comparative number or at least resistance of the channels along which excitatory impulses are propagated from the excited to the observed area. Further, by means of carefully planned interruptions, we hoped to ascertain how far such impulses

were limited, presumably by the anatomical relations of the paths along which they were conducted, to given tracts of fibres in the different columns. We thus designed our work to ascertain the scheme upon which the fibrous structure of the cord was arranged, and this for both ascending and descending impulses.

We found that the electrometer was not a suitable instrument for this investigation, since with minimal stimulation its movements were too small to admit of sufficiently accurate estimation, whilst the uncertainties connected with the conditions regulating its sensibility rendered exact comparisons of small differences between different sets of experiments impossible. We therefore used the galvanometer in all the remaining experiments, obtaining with it results which could be better relied upon for purposes of comparison.

## SECTION 5 — ELECTRICAL CHANGES PRODUCED BY LOCALISED STIMULATION OF THE COLUMNS OF THE CORD.

### *Plan of Experiments.*

In order to obtain quantitative comparisons between the effects evoked by localised excitation of different columns in the cord, the plan adopted was to divide the cord in the mid-dorsal and lumbar regions, and prepare one end of the isolated experimental tract lying between the sections for connection with the galvanometer electrodes and the other for excitation. The method of connection has been already fully described, namely, at the cross section and the surface 1 centim away, by means of cables, under all precautions previously indicated. The preparation of the other end for excitation was effected by removing about a centimetre from the end, and thus exposing the cross section of the cord, in which it was possible, using the precautions described in the chapter on operative procedure, to stimulate, with a pair of fine platinum electrodes, the section of each column thus exposed, anterior, lateral, posterior, or the grey matter.

The experiments showed us that with moderate intensities of stimulating currents, electrical effects were always produced in the observed end of the experimental tract, when at the other end the cross section of either lateral or posterior column was excited, but that only very small and rare effects were caused by a similar excitation of the anterior columns or of the grey matter. This suggested that no continuous strand of fibres united the excited portion of these latter tracts with the observed portion. We shall refer to this result again later on, since, however, the stimulation of the lateral and posterior columns alone gave notable effects, we limited our excitation in the majority of instances to these columns.

The majority of these experiments were carried out on Cats (17 animals), but we also made a considerable number of experiments on three large Macaque Monkeys. It will be presently seen that the results differ in the two animals in a most interesting way.

The experiments all fall into two great groups, distinguished by the fact that in one the lumbar end of the isolated fragment of cord was the seat of galvanometric observation, whilst, in the other, the dorsal end was observed and the lumbar end excited. In the first case the electrical changes are obviously due to the discharge of nerve impulses *down* the cord, in the second to their discharge *up* the cord.

We will now proceed to a detailed description, first of a typical experiment, and then of the results obtained from several experiments under these two opposite conditions, and we will take first the case of impulses descending the cord, these impulses having been produced by excitation of some one column, as displayed in the dorsal section of the "experimental region" of cord. The galvanometric connections having been made with the lower lumbar end of this tract, electrical changes were evidenced in it when the descending impulses reached that part which was in connection with the electrodes leading to the instrument.

## SECTION 6 — ELECTRICAL EFFECTS EVOKED IN THE LUMBAR CORD BY EXCITATION OF THE COLUMNS IN THE DORSAL REGION

### (a) *Typical Experiments*

Since the results in the case of Cat's cord, as mentioned in the preceding paragraph, are different from those obtained with the Monkey's cord, it is desirable to separate out the experiments made upon each. We will therefore describe a single typical experiment and its results in the case of these animals. In order to avoid repetition, the general procedure, which is the same in both animals, will be described more minutely in the case of the Cat (this being taken first) than in that of the Monkey. To make clear the relationship of the excitation to the galvanometric connections, the actual positions in a typical case of the seat of operation and of both sets of electrodes is given in fig. 10, p 368, which represents the spinal cord of an animal thus experimented upon.

The cord of the Cat (243) was divided at the level of the 7th dorsal vertebra, it was then exposed in the lumbar region for 3 centims and divided at the level of the 3rd lumbar vertebra, thus isolating an experimental region which extended between these two levels. The distal (lumbar) end of this isolated fragment was now ligatured, and all connections having been divided, was raised in air by the thread. By means of cables the transverse section was connected with one non-polarisable electrode, the longitudinal surface at 1 centim distance by a similar cable with the other. The electrodes were fixed, as before, on a stand, and arranged at such a height that a considerable length, two or three inches, of thread cable hung loosely between them and the cord, all error due to mechanical displacement, as in the cortical experiments, being thus guarded against. The upper end of the isolated fragment or experimental

tract of cord was now exposed for about a centimetre, and a fresh division made so as to expose a more excitable section for stimulation

The portion of cord investigated showed, when connected with the galvanometer, the usual resting electrical difference between the surface and ligatured cut end (see Chapter IV.)

When after compensation the galvanometer needle was steady, the exciting electrodes, guarded by a short-circuiting key, were carefully held by one observer against the cut end of one column of the cord, as described in Chapter III, every precaution being taken to ensure that the surface should be dry. The key was now opened by the observer at the galvanometer, and by means of the revolving paraffin key the column was stimulated for a definite time ( $3\frac{1}{2}$  seconds in this case), by a series of weak induction currents (100 per second) produced by the usual magnetic interruptor, and made equal and alternate by means of the Helmholtz side-wire. The intensity of the exciting currents had to be adapted to the varying condition of the animal, etherisation, &c, but the results aimed at being to stimulate the fibres in the separate columns rather than to arouse the reflex activity of the cord, it was thought advisable, at any rate in the commencement of an experiment, to use currents only just sufficient to evoke definite effects, such excitation will be termed here "minimal"

In this particular case one Daniell cell was used in the primary exciting circuit and the secondary coil stood at 500. The excitation of either anterior column produced no electrical change, that of either lateral produced a very distinct effect, of the usual excitatory character, that is, an effect which commenced with the stimulation and did not persist after its cessation.

The effect indicated the establishment of a transient electrical state, opposed in direction to that of the original resting difference. The galvanometer deflection, which recorded the change, was very distinct in its commencement and termination, so that its amount could be determined with accuracy. The deflection was 41 when the left, and 57 when the right lateral column was excited. The stimulation, in exactly the same way, of the cut end of the posterior columns produced much more pronounced effects, amounting to 96 in the case of the left, and 94 in that of the right column. Every precaution was taken to ensure that as far as possible the degree of narcosis, &c, should be the same during the four stimulations, and an interval of 1 minute was generally allowed to elapse between the successive applications of each.

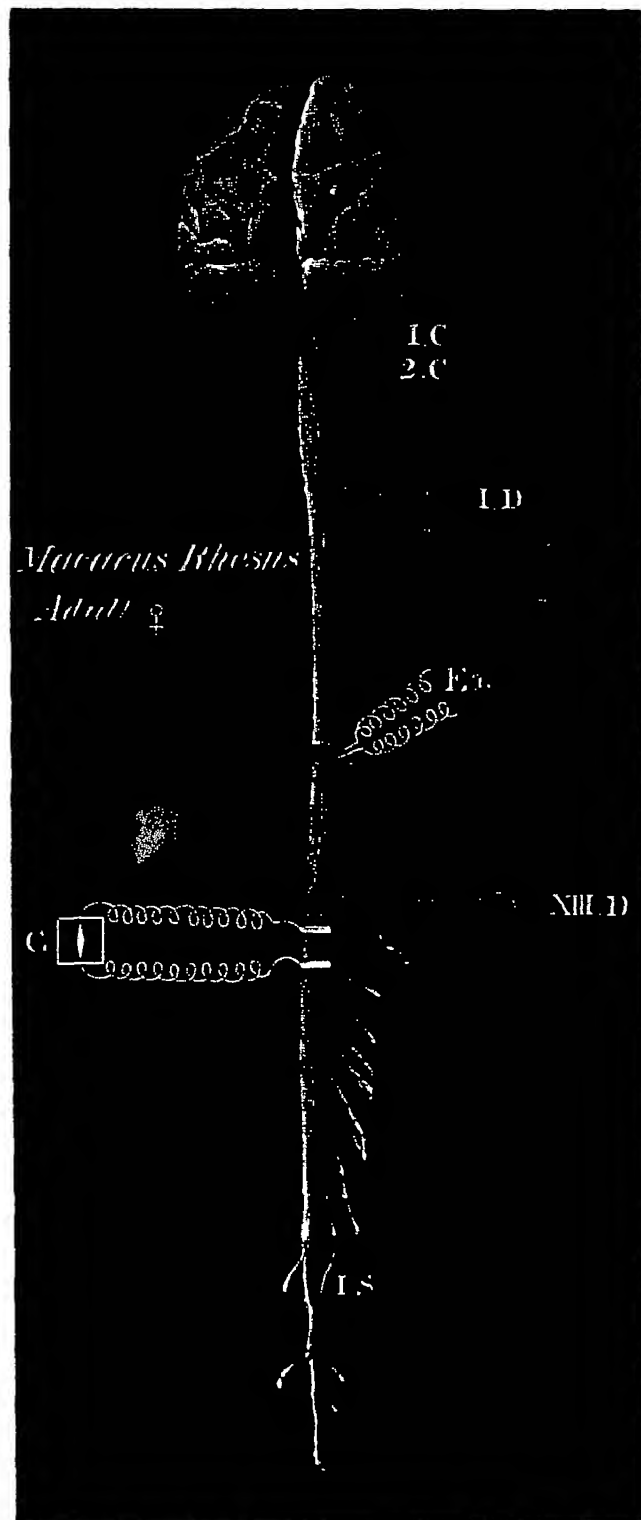
When a stronger stimulus (double the strength, coil 1000), of precisely the same character and duration was employed, larger effects of the same kind were produced, stimulation of the anterior regions being again followed by only a mere trace of effect, that of either lateral by well-marked deflections (left 105, right 140); and that of the posteriors by very large deflections (left 290, right 208).

It will be seen that this relationship of magnitude of effect is one which is retained in all the results obtained in this way by differential columnar excitation of the divided cord of the Cat.

A very different relationship is, however, found to exist when the spinal cord of the Monkey is investigated in a similar way.

The spinal cord of a Macaque Monkey (232) was divided at the 10th dorsal vertebra for excitation, and also at the 2nd lumbar, where having been freed from its nervous

Fig 12



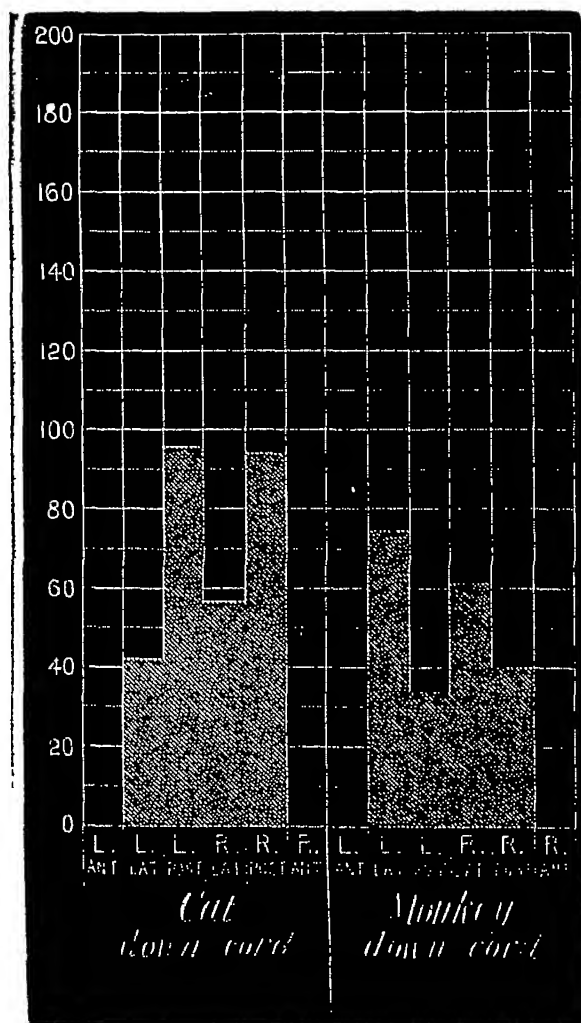
and other attachments, it was ligatured near its divided end, raised as in the preceding experiment, and by means of cables connected with the leading off non-polarisable electrodes at its ligatured end and at its surface (see fig. 12).

The usual resting electrical difference was observed when the electrodes were connected with the galvanometer, and was compensated. Each column was now

excited where it had been exposed in the dorsal cross section, the excitation being as in the preceding case, viz, that of the interrupted induction currents (100 per second) with the Helmholtz side-wire, and the period of excitation being  $3\frac{1}{2}$  seconds

As in the Cat, the excitation of either anterior column produced no effect, that of each lateral, however, evoked a marked electrical effect, the two laterals giving respectively, left 75 and right 62, the deflection being in each case opposed in direction to that of the resting difference. Excitation of either posterior column was followed by a much smaller deflection than the corresponding lateral, the left giving 34, the right 40

Fig 13



When a stimulus of double the strength (coil 1000) but of the same duration was employed, very large deflections were produced, but the relationship of the results still held good, as excitation of the left lateral gave 210, whilst that of the corresponding posterior gave 165, and similarly excitation of the right lateral gave 140, whilst that of the corresponding posterior gave 120.

If the comparative value of the electrical change produced in the cord by "minimal" excitation of the different columns be represented graphically, as in the annexed figure, a glance is sufficient to show the striking contrast between the result obtained in the Cat and that obtained in the Monkey, since in the latter case the laterals pre-  
over the posteriors. (See fig. 13.)



*(b) Average of Experiments*

The two experiments just described are types of all those made upon normal animals. The following table gives the results of the readings obtained in four Cats and one Monkey, with stimuli which were varied in one particular only, that of intensity

It will be noticed that the average in the Cat of the deflections produced by excitation of the posterior columns is twice as great as that following stimulation of the laterals

In the Monkey, on the other hand, the average of the stimulation effects obtained from the lateral is about half as large again as that produced by the excitation of the posterior columns

EXCITATION of Cut Dorsal Cord (Peripheral Surface)    Electrical Effect in  
Lumbar Cord.

	Region observed	Region excited	Intensity of stimulus	Electrical effects evoked by stimulation of					
				Left			Right		
				Ant	Lat	Post	Ant	Lat	Post
Cat (243)	2 Lumbar	8 D	500 min	trace	41	96	trace	57	94
" "	"	"	1000 max	"	105	290	"	140	208
" (351)	1 "	7 D	250 min	"	33	70	"	55	62
" "	"	"	"	"	12	39	"	42	52
" "	"	"	500 max.	"	90	170	"	"	"
" "	"	"	"	"	31	70	"	90	105
" "	"	"	"	"	56	110	"	91	115
" (230)	13 Dorsal	10 D	500 min	"	30	130	"	65	150
" (378)	3 Lumbar	"	"	"	48	86	"	41	123
" "	"	"	"	"	48	92	"	32	105
" "	"	"	1000 max	"	39	225	"	62	197
" "	"	"	"	"	75	175	"	98	207
					608	1553		773	1418
General				average	51	129	"	70	129
Monkey (232)	2 Lumbar	10 D	500	"	75	34	"	62	40
" "	"	"	"	"	98	22	"	65	30
" "	"	"	1000	"	210	165	"	140	120
General				average	128	74	"	89	63

A further result which an analysis of these effects shows, is the difference between the average deflection in the case of the posterior and the lateral column with weak minimal stimulation and maximal stimulation respectively.

AVERAGE effect evoked by stimulation of one lateral column

	Cat	Monkey
Minimal stimulation	42	75
Maximal       ,,	87	175

AVERAGE effect evoked by stimulation of one posterior column

	Cat	Monkey
Minimal stimulation	92	31
Maximal       ,,	170	142

It is seen that in the Cat both minimal and maximal stimulation evoke effects which are twice as large in the case of the posterior columns as in that of the laterals.

In the Monkey the lateral column effect with minimal stimulation is, on the other hand, twice as large as that produced by the stimulation of the posterior column, but with a stronger stimulus this relationship does not hold, owing, possibly, to the increased reflex discharge which excitation of the posterior column now evokes

The difference between the results of excitation of the columns in the two animals is, therefore, best marked with the weaker intensity of stimulus. It is evident that this must depend upon the number of fibres which form direct connections between the excited dorsal and observed lumbar region, along which fibres as constituting paths of least resistance the nerve impulses are almost entirely propagated from the excited area, when the fibres this contains are aroused by a weak stimulus

This seems to us to afford an experimental proof of the relatively larger number of continuous lateral column-fibres which must exist in the Monkey as compared with the Cat; this greater proportion may, in the light of the previous results described under cortical stimulation (Chapter V), be ascribed to the more complete development of the fibres forming the pyramidal tracts

The histological investigation of the fibres in the tract in the two animals seems to support this view, there being apparently many more fibres in the pyramidal tract of the Monkey than in that of the Dog, as determined by the degeneration method. It is, moreover, to be expected that the fibres in question must increase in number with the completeness of the differentiation of those cortical structures from which

they spring, and it need hardly be pointed out that, whilst minute localisation of representation of movements on the cortex of the Monkey has been clearly demonstrated, such perfect differentiation has not been found in the Carnivora.

We will now pass on to the consideration of the results obtained when the dorsal portion of the experimental tract of the cord is connected with the galvanometer, and the columns excited in the lumbar region, thus evoking impulses which, to produce effects, must pass *up* the cord.

#### SECTION 7 — ELECTRICAL EXCITATION EFFECTS EVOKED IN THE DORSAL REGION OF THE CORD BY EXCITATION OF THE COLUMNS IN THE LUMBAR REGION

In these experiments the cord was divided in two places, as described in the preceding paragraphs; but, since the electrical effects in the dorsal end of the tract thus isolated were to be investigated, the cord was prepared for several centimetres at the upper dorsal level. At the lower lumbar section the cord was prepared by excision of one centimetre for purposes of excitation. The exciting and galvanometric arrangements were of the same character as before, their relative disposition being sufficiently indicated in the annexed fig. 14.

##### (a) *Typical Experiments.*

We will again first describe the results of an experiment selected as a typical one, and carried out on the spinal cord of the Cat (244), as follows —

The cord was divided at the 7th dorsal vertebra and prepared for observation as before described. It was then divided at the 2nd lumbar vertebra for excitation.

The upper end of this experimental tract showed the usual resting electrical difference between surface and cross section, which was compensated.

The cut lumbar surface of each different column was now excited for  $3\frac{1}{2}$  seconds by the interrupted current, 100 per second (Helmholtz side-wire), and the galvanometric effect observed.

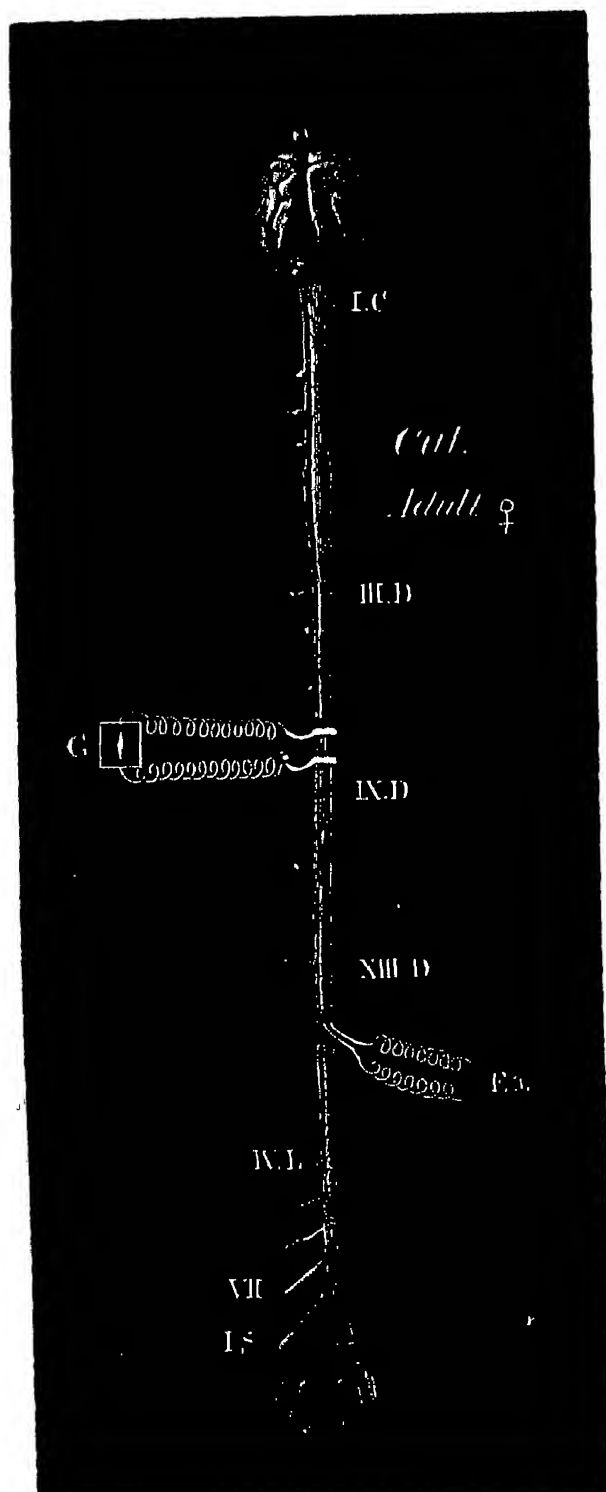
Although the secondary coil stood at only 500, the preparation was very excitable. Excitation of the anterior columns was followed by a slight but distinct effect, 22 with left side, 28 with the right, these, however, did not occur on repetition, and are exceptional.

On exciting the left lateral column, a deflection\* of 120 was observed, whilst on exciting the left posterior column, a deflection of 215 was produced; finally excitation of the right lateral was followed by 100, of the right posterior, by 190.

The general relationship of magnitude of electrical change evoked in the cord of the Cat by lumbar excitation of the cross sectional area of its different columns is thus the same as that obtained by dorsal excitation.

That is to say, whether the nerve impulses proceed down the cord from an upper excited to a lower observed area, or up from a lower excited to an upper observed area, the anterior column fibres give no effects or only small ones, the lateral give marked effects, but the posterior give still more pronounced effects.

Fig 14

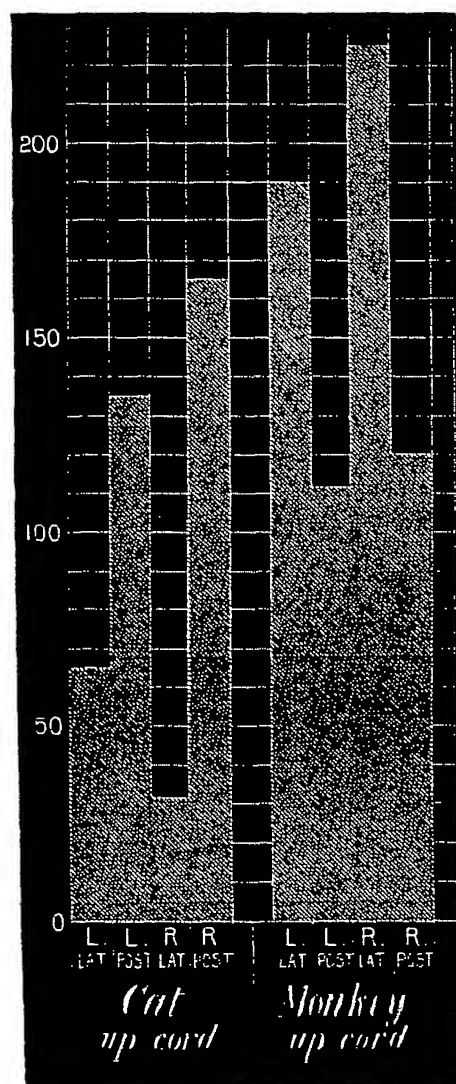


If we turn now to experiments upon the Monkey's cord, the same contrast with the results in the Cat appears as was described before. Thus in a Macaque Monkey (271) the cord was exposed and divided at the 8th dorsal vertebra and was then freed from its attachments, ligatured on the peripheral side of the section and raised

from the canal, it was then connected with the electrodes exactly as in the case of the Cat

The lower section and exposure occurred at the level of the 1st lumbar, and the cut surface of the columns was then stimulated as in the preceding case. The necessary strength for minimal excitation was only found when the coil was 2000. The anterior columns evoked no definite effect, but excitation of the laterals evoked large effects, left 190, right 225, whilst similar excitation of the posteriors evoked smaller deflections, left 112, and right 120

Fig 15



The results of these two typical experiments will be rendered still more obvious by the annexed figure, in which the value of the excitatory effects in the Cat and Monkey are displayed in a graphic form. It will be seen how completely the relative size of the effect evoked by stimulation of the two kinds of column is reversed in the two animals. (See fig 15)

(b.) *Average of Experiments*

We will now take the average of the observations in which the condition of the animal, &c, was, as far as possible, the same throughout, and the effect evoked in the dorsal cord by stimulating the lumbar columns accurately noted

## EXCITATION of Cut Lumbar Cord (Central Surface). Electrical Effect in Dorsal Cord

	Region observed	Region excited	Intensity of stimulus	Electrical effects evoked by stimulation of					
				Left			Right		
				Ant	Lat	Post	Ant	Lat	Post
Cat (197)	10 dorsal	1 lumbar	2000 max	0	64	135	0	32	165
Cat (244)	8 dorsal	"	500 "	trace	80	120	trace	95	160
"	"	"	" "	22	120	215	28	100	190
"	"	"	" "	0	126	120	14	66	100
"	"	"	" "		160	230		125	140
Cat (256)	8 dorsal	3 lumbar	300 min	.	65	76		20	90
Cat (355)	8 dorsal	2 lumbar	1000 max	.	65	80		140	82
"	"	"	" "	.	80	50		142	105
"	"	"	" "	.	110	151	.	115	175
Cat (375)	9 dorsal	2 lumbar	500 "	.	145	125	.	145	78
"	"	"	250 min	.	61	46		41	54
"	"	"	500 "	.	60	82		81	98
"	"	"	1000	.	192	273		165	295
"	"	"	1000	.	243	295	.	210	410
"	"	"	500		190	140		68	215
					1761	2138	..	1545	2357
			Average	..	117	148	.	103	157
Monkey (233)	7 dorsal	1 lumbar	2000			.		120	92
			2000					75	20
Monkey (271)	8 "	2 "	2000	.	190	112	..	225	120
			Average	.	190	112		140	77

It will be noticed that the general relationship holds in the case of impulses passing up the cord, namely, that in the Monkey the most marked effects are evoked by excitation of the lateral, in the Cat by excitation of the posterior columns. There are, however, differences in the precise characters of the relationship as compared with that indicated in the preceding group of observations when the nerve impulses were descending. These differences are exhibited by separating all the lateral and posterior column effects, in accordance as they were obtained with the minimal and maximal stimulation, respectively.

## EXCITATION of Lumbar Cord. Electrical Effect in Dorsal Cord.

*Cat.*—Average effect evoked in the Cat by stimulation of one lateral column.

Minimal stimulation . . . . .	55
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Maximal „ . . . . .	124
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Average effect evoked in the Cat by stimulation of one posterior column

Minimal stimulation . . . . .	74
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Maximal „ . . . . .	164
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*Monkey* —Average effect evoked by stimulation of one lateral column

Maximal stimulation . . . . .	133
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Average effect evoked by stimulation of one posterior column

Maximal stimulation . . . . .	86
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The chief differences between these results obtained when nerve impulses proceeded up the cord and those obtained when they travelled down, are the following —

(1.) The maximal effect in the Cat is more than twice as great as the minimal with stimulation of both lateral and posterior columns when the impulses are ascending, *i.e.*, the lumbar end excited. On the other hand, when the impulses are descending the maximal effect was less than twice as great. There is thus a gain in the amount of the effect, when the stimulus is on the lumbar side of the region, in proportion as the excitation increases in intensity.

(2) The minimal posterior column effect with ascending impulses is larger than the lateral in the Cat in the proportion of 3 to 2, but this proportion is less than that obtained when the dorsal cord was excited and descending impulses evoked, since this was 2 to 1.

(3) In the Monkey the lateral column effect is larger than the posterior in the proportion of 3 to 2, when ascending impulses are evoked by maximal stimulation; with descending impulses similarly evoked the proportion is 9 to 7.

The characteristic predominance of the lateral column of the Monkey is however marked, whether the excitation is dorsal and the descending impulses investigated, or lumbar as in the present case, and the ascending effects observed.

The differences above described seem to indicate that the generated impulses travel not only along direct but indirect paths, that is along paths involving cells, and that the structural relations and physiological effects of the interposed structures are such that these influence, in both animals, traversing nerve impulses differently according as their direction is centripetal or centrifugal. It is particularly as regards the lateral column effect that this influence of direction is most marked, it would, therefore, seem that the lateral column comprises among its fibres some (presumably internuncial) which offer less resistance to ascending than to descending impulses. This view will receive confirmation, and be again referred to in the later experiments on the relations of the cord to the nerves. (See Chapters IX. and X.) It is sup-



ported by the series of experiments to be next detailed, in which the result of intervening localised section of columns upon the electrical effects evoked by excitation of the same is set forth

#### SECTION 8 —THE ELECTRICAL CHANGES IN EACH HALF OF THE LONGITUDINALLY DIVIDED CORD

The question as to what amount of the electrical effects, and thus of the excitatory processes underlying these, when evoked by stimulation of one column, is due to changes confined to that column only, is one of such importance in respect to the well-known views as to conduction by the different groups of fibres in the cord that it seemed advisable to approach this subject by particular experiments. In the case of the changes in the cord following excitation of the cortex, we had found that it was possible to split the cord longitudinally without destroying the excitability of the two halves, and so to obtain evidence of unilateral localisation of effect. This seemed the most straightforward means of getting information as to localisation when the columns of the cord were the seat of the excitation, at the same time we felt that the operation of longitudinal division must in all probability seriously affect the functional continuity of the posterior columns, whose excitation in the Cat, as the foregoing experiments have shown, is productive of such marked results. To these experiments attention must now be given.

We have only performed two successful experiments, both upon the Cat.

In the first the cord was divided at the 9th dorsal and at the 4th lumbar vertebræ. The upper dorsal end of the fragment was prepared for excitation, the lower lumbar end was freed and split in a manner similar to that employed in the cortical experiments (See fig. 16.) Each half was connected with a pair of non-polarisable electrodes, as in those experiments, and either pair could be switched into the galvanometer circuit and its electrical changes observed. The general arrangement of the circuit in this case is shown in fig. 1.

When the columns were excited for 5 seconds with the secondary coil at 2000, and the right portion of cord investigated, then—

Excitation of the right lateral produced an effect of 31,  
left        „        „        no effect.

On the other hand,

Excitation of the right posterior produced an effect of 53,  
„        „        left        „        „        „        15.

The left portion of cord was now investigated and the same strength of stimulus employed. It was found that—

Excitation of left lateral produced effect of 42, 56

„	right	„	„	„	6	0
„	left posterior	„	„	„	87	
„	right	„	„	„	45	

IC

*Cat.*  
*Adult ♀*

Exc. to G. IX.D

to G. XIII

IV.L. to G.

VII

On repeating this experiment with a stronger stimulus (coil 3000), the unilateral character of the right lateral column became less marked, whilst the left and right posterior columns gave now equal bilateral results; thus—

Excitation of left lateral produced effect of 68

„	right	„	„	„	36
„	left posterior	„	„	„	96
„	right	„	„	„	89

Fig 17

*Cat.*  
*Adult*



XIII.D



It thus appears that when half the split cord is observed and the columns excited on the central side, the excitatory electrical change, produced by weak excitation of the lateral column is entirely confined to the side stimulated, whilst that produced by similar excitation of the posterior column is but mainly confined to the stimulated side, while when the excitation is of sufficient intensity it is produced equally on

both sides. This, therefore, suggests that descending impulses in the lateral column are, to a very large extent, confined to these fibres, but those in the posterior column cross into similarly situated fibres on the opposite half of the cord.

A second experiment of the reverse kind was made on another occasion, the excitation being now in the lumbar region, and the impulses evoked thus being ascending. The cord was divided at the 7th dorsal and 3rd lumbar, and the upper dorsal portion was prepared for galvanometric observation, and split longitudinally, whilst the lower lumbar portion was prepared for excitation, the general arrangement is shown in fig 17.

When the right half of the split cord was examined—

Excitation of the right lateral produced an effect of 38

„	left	„	„	„	3
„	right posterior	„	„	„	40
„	left	„	„	„	14

The cord was then again divided a little centrally to the seat of the previous excitation, so as to expose a fresh surface for the stimulation, and now—

Excitation of right lateral produced effects of 86 , 94

„	left	„	„	„	16	15
„	right posterior	„	„	„	81	112
„	left	„	„	„	52	60

The left half of the cord when observed gave the following results —

Excitation of left lateral produced effect of 33

„	right	„	„	„	3
„	left posterior	„	„	„	40
„	right	„	„	„	7

The general conclusion to be derived from these experiments is that the excitation of the lateral column produces an effect which is limited to a very remarkable degree to the side excited. On the other hand, the excitation of one posterior column produces with appropriate excitation bilateral electrical effects, but the effect is twice as great on the same side as it is on the opposite one.

It must, however, be borne in mind that the operation may, by depressing the excitability of the posterior columns, be a source of error which can interfere largely with the above results, since the posterior columns are more liable than the lateral to suffer by the procedure of splitting, and earlier experiments have convinced us that if they are injured the electrical change produced by their excitation is very largely affected.

The extent to which the effects and thus the nerve impulses are localised in the

columns excited was, therefore, now approached by another method, that, namely, of intervening sections

## SECTION 9 — INFLUENCE OF INTERVENING SECTIONS UPON THE ELECTRICAL CHANGE IN THE CORD FOLLOWING EXCITATION OF THE DIFFERENT COLUMNS

The extent to which the electrical change in the cord following excitation of the cut columns is dependent upon direct continuity of nerve fibres between the part of the column excited and the part of the cord observed is more clearly indicated by the experiments now to be described

In these the excitatory and galvanometric arrangements were similar in all details to those employed in the two preceding groups of experiments, but the experimental tract had been subjected to important additional operations, some particular column indicated being divided at a position intervening between the region of excitation and the observed region, and the result of such division as affecting the electrical excitatory change being then estimated

The section, the influence of which was thus investigated, was made in most cases at the time of the experiment. In a few cases the section was made three or four weeks beforehand, in order not only to ensure a more striking alteration of effect by the degeneration of the continuous nerve tracts involved, but also to provide against any transient disturbance due to the operation, affecting the excitability both of the particular tract and of other nerve tracts than the one operated upon

Since the influence of each separate intervening section had to be studied in the case of excitation evoking both descending and ascending impulses in the experimental tract, the experimental results of any section naturally fall into the two groups already indicated in the preceding Sections.

### (1.) *Electrical Effects in the Lumbar Cord Evoked by Excitation of the Dorsal Cord.*

#### A. *Influence of Hemisection.*

The experiments were made upon three animals (Cats), in all of which the intervening hemisection occurred at the level of the 12th dorsal vertebra, in the first on the right side, in the second and third on the left side

Each experiment was conducted precisely as those previously described; that is to say, the cord was divided at the 8th dorsal and 2nd lumbar vertebræ. The lower end of the experimental tract was prepared for connection with the galvanometric electrodes, the upper for excitation. The different columns were first successively excited before the hemisection in the usual manner, and the electrical effects observed. These are shown in the preceding table, see page 381, and were of the kind indicated in Section 6 (b). The cord was now exposed at the 12th dorsal, the section made and the electrical effects of the excitation of the different columns

under these circumstances were then noted The following is a table showing the results obtained —

ELECTRICAL Effects in Lumbar Cord Evoked by Excitation of Dorsal Cord after  
Intervening Hemisection on the Right Side at 12th Dorsal Vertebra

	Region observed	Region excited	Stimulus	Electrical effects			
				Left		Right	
				Lat	Post	Lat	Post
Cat (351)	2nd lumbar	7th dorsal	500 min	45	71	0	0
			„ min	62	45	0	0
			„ min	43	55	0	0
			1000 max	100	81	0	0
			2000 max	201	145	6	26
			2000 max	180	145	12	31

INTERVENING Hemisection on Left Side at 12th Dorsal

	Region observed	Region excited	Stimulus	Electrical effects			
				Left		Right	
				Lat	Post	Lat	Post
Cat (371)	1st lumbar	8th dorsal	500	18	0	132	56
			„	18	0	126	75
			„	15	12	110	58
			1000	49	26	201	193
			„	29	26	184	182
Cat (278)	3rd lumbar	9th dorsal	500	0	0	47	56
			1000	19	34	148	198

The average results of the excitation of the lateral and posterior columns, when grouped, as dependent upon the intensity of the stimulus, show the following quantitative comparison

AVERAGE Effects obtained by Exciting Columns on Side of Section.

	Minimal stimulation	Maximal stimulation
Lateral . . . .	8	23
Posterior . . . .	2	29

## AVERAGE Effects obtained by Exciting Columns on Opposite Side to Section

	Minimal stimulation	Maximal stimulation
Lateral	74	183
Posterior	62	173

From this table it will be seen that the electrical effects observed in the dorsal region are profoundly modified by an intervening hemisection of the cord. With an excitation of minimal intensity, the application of the stimulus to the columns at the dorsal end situated on the side of the section evokes little or no electrical effect in the lumbar region. The interruption of the directly continuous fibres by the hemisection has thus reduced the effect to such an extent, that in two Cats it was completely abolished, and only present in one.

With the same minimal intensity of stimulus, excitation of the posterior column evoked no effect at all, except in one instance; the interruption in the fibres of this column thus abolishes the electrical effect.

With a minimal stimulus, therefore, the electrical effect in the lumbar region obtained by excitation of the columns in the dorsal region is dependent upon an unbroken continuity in the fibres descending along the same side as the excited column. It is thus clear, that not only are the stimulating induction currents which traverse the excited end of the exposed column confined to that side of the cord, but, in addition, that the nerve impulses generated by this stimulus travel down that side, since it is the arrival of the nerve impulses at the lumbar end of the tract which produces the electrical effect and this is practically abolished by the interruption offered by the hemisection.

Whilst the experiments thus furnish strong evidence against any direct and continuous tract of nerve fibres passing from one side of the cord to the other, the presence of effects on the two sides of the cord, when evoked by more intense stimuli, shows that the interruption of hemisection is not a complete block. With increasing intensity it will be noticed that excitation of both lateral and posterior columns on the side of section evoke electrical effects in the cord below. These must be due to the passage of nerve impulses from the excited area along paths which are in relation with cells, i.e., indirect, since these are the only known channels across the cord. These impulses may discharge, in a reflex manner, the cellular energy of both sides of the cord, the opposite side in a much less degree than the same side; a crossed electrical change would then indicate the sum of the nerve impulses evoked in the opposite side by a discharge of nerve cells. Similar effects would, however, be obtained if, without any reflex influence being present, an indirect path crossed from the columns of one side to a column of fibres on the opposite side. Both agencies may



be presumed to operate in these cases, though the results of the experimental observations set forth in the succeeding chapters all favour the supposition that the fibres which form the indirect crossed path are almost entirely derived from the posterior column, whilst the internuncial fibres, by which the successive segmental groups of cells are associated with one another, are mainly confined to the lateral column. It will be observed that the *crossed* effect is only  $\frac{1}{8}$  to  $\frac{1}{6}$  of the direct effect evoked by stimulation of the side opposite to the lesion, hence either the nerve impulses, of which the effect is the index, are either greatly reduced in quantity by their passage through the grey matter, or comparatively few nerve impulses take this crossed path.

Finally, as regards the effects in the side opposite to the lesion, it will be noticed that, comparing the relative value of the two effects, due to excitation of the posterior column is now less than that of the lateral column. This is probably due to the necessary exposure of the columns at the 12th dorsal vertebra acting injuriously upon the excitability and conductivity of the exposed but otherwise uninjured posterior column not included in the section.

A glance at the full details of experiments 351 and 371 will show (see table, Section 6 (b)), that the same relation was present in most cases before the hemisection was made; the subject will be referred to in more detail in the next paragraph, which deals with the result of section and injury to the posterior columns.

### B. *Influence of Section of Posterior Columns.*

The influence of the section of both posterior columns in the lower dorsal region upon the electrical effect evoked in the lumbar region, and thus upon descending nerve impulses, is shown by the following experiment —

The cord was divided in a Cat (357) at the 9th dorsal and at the 2nd lumbar vertebræ, it was prepared for excitation at the former region, for attachment to the galvanometric electrodes at the latter. The cord was then also exposed at the 11th dorsal vertebra, and, before any operative lesion, an experiment of the customary kind was made. The excitation, with stimulus 500 of the two laterals, gave deflections of 30 and 65, average, 47, that of the two posteriors gave 130 and 150, average, 140. After division of both posterior columns at the 11th dorsal, similar excitation of the lateral columns evoked effects of 60 and 105, average, 82,\* whilst that of either posterior column evoked no effect whatever, unfortunately, the effects evoked by stronger stimuli were not observed.

The interruption, therefore, as regards the posterior columns was complete with this intensity of stimulus, and hence all nerve impulses generated by such "minimal" excitation of either column in the dorsal region are propagated to the lumbar region.

\* It will be seen that the average effect obtained due to excitation of the lateral columns after section of the posterior columns is increased. A similar exaltation occurs in the experiments detailed in Chapter IX, Section 7, C, where the causation of the phenomenon is discussed.

along fibres which do not pass out of these columns, and a strict localisation of nerve impulses is with this intensity of stimulus possible

The posterior columns are particularly susceptible to injury, since they are especially exposed to danger of drying, &c, in the preparation of the cord. This circumstance must be always kept in view when experiments involving an intervening exposure of the cord are made. We were much puzzled by the result of two experiments in which, after dividing the cord in the dorsal and lumbar regions, we had exposed a portion of the experimental tract in the intervening part, about the 12th dorsal, for subsequent operative lesion. The following results were obtained —

	Dorsal cord excited		Stimulus	Lumbar cord observed				
	Observed end	Excited end		Left		Right		
				Lat.	Post	Lat	Post	
Cat (316)	2nd lumbar	8th dorsal	min	90	31	103	28	
			max	190	91	130	85	
			max	165	65	98	115	
Cat (371)	1st lumbar	9th dorsal	min	145	112	140	124	
			min	132	98	144	104	
			max	170	190	210	182	
			max	280	145	192	195	
			max	142	179	153	205	
			min.	62	42	73	30	
			General average		153	106	141	117

In these cases therefore all lateral column effects average with minimal stimulus 111, with maximal 166; whilst all posterior column effects average with minimal stimulus 70, with maximal 145. It is seen that these results are exceptions to the general rule (see p. 385) of the effect from the posterior being in the Cat larger than that from the lateral. That this was really due to the prolonged exposure at the 12th dorsal injuriously affecting the posterior columns is shown by the fact that such exceptional results were only obtained when an intervening portion had been thus exposed. If prolonged exposure is avoided by performing the necessary operation immediately before the desired intervening lesions are to be made no such lowering of the amount of the posterior column effect is observed. In this relation it is possible to explain the comparatively small posterior column effect (see p. 385) of the Monkey as in some measure due to a loss of excitability in these columns, which seem to be much more susceptible than the laterals (CHAUVEAU).

*Influence of Section of one Posterior Column.*—It is possible to interrupt one column only, and thus to obtain conclusive evidence of the extent to which the

electrical effects evoked by its stimulation are due to the propagation of impulses along fibres which are confined to the column

This lesion was effected in three Cats on the left side, the results are seen in the following table —

ELECTRICAL Effect obtained in the Lumbar Cord by Excitation of Columns in the Dorsal Region after intervening Section of Left Posterior Column

			Stimulus,	Left		Right	
				Lat	Post	Lat	Post
Cat (357)	2nd lumbar	10th dorsal	500 min	68	12	82	48
			„ min	75	14	120	70
Cat (371)	1st lumbar	9th dorsal	250 min	86	0	89	34
			500 min	115	0	145	66
			1000 max	198	45	180	170
			„ max	169	26	146	130
Cat (378)			500 min	59	3	75	26
			1000 max	144	34	131	193

AVERAGE Effect obtained from Side of Section.

	Minimal stimulation	Maximal stimulation
Lateral . Posterior	80 6	170 35

AVERAGE of Effect obtained from Side Opposite Section

	Minimal stimulation	Maximal stimulation
Lateral Posterior	102 51	152 154

It will be noticed that with minimal stimulation the interruption occasioned by the unilateral section is almost complete, hence we conclude that—

(a) The stimulation must be localised to the column on which the electrodes are placed;

(b) The electrical effect in the lumbar cord, following excitation of one posterior column, must be due to nerve impulses proceeding down channels confined to that column;

(c) No tract of fibres in other columns can have direct and continuous connections with the fibres in one posterior column.

With maximal intensity of stimulation the interruption is sufficient to lower the posterior effect in the proportion of 164 (that of the uninjured posterior) to 35, that is, 80 per cent. The effect still obtained, in spite of the interruption, must be due to indirect paths which come into relation with cells; these paths may partly cross or be continuous with fibres contained in the uninterrupted lateral columns on the side of the lesion. The next experiment to be detailed (C) will throw some light upon this point.

### C *Influence of Section of both Posterior Columns and one Lateral*

By making a hemisection and then dividing the remaining posterior column, a lesion is made (MIESCHER) in which the only intact fibres in the cord are those of one lateral column, one anterior column, and the fibres in one half of the grey matter.

Such a lesion was made in two animals at the 12th dorsal vertebra, with the following result on the electrical changes in the lumbar cord.

#### HEMISECTION on the right side and section of the left posterior column.

	Cord observed	Cord excited	Stimulus	Left		Right	
				Lat	Post	Lat,	Post
Cat (357)	2nd lumbar	9th dorsal	500 min	90	0	0	0
			"	75	0	0	0
Cat (351)	3rd lumbar	7th dorsal	2000 max	140	32	11	16
				135			
				125			

It will be seen that with a "minimal" stimulus no electrical effect was evoked except by excitation of that lateral column (left) which remained intact. Hence, the lateral column minimal effect is as strictly localised to its contained fibres as that of the posterior column, and the presumption is that it contains no fibres which are directly continuous with those which form at the level of the 9th dorsal the other lateral and the two posterior columns.

On the other hand, with a maximal stimulus, excitation of each column evokes an effect, which is, however, much less pronounced than that obtained by the excitation of the uninterrupted lateral. It will be noticed that the posterior column on the side of the uninterrupted lateral gives far the most marked of these effects. If the effects are taken to mean that there exist indirect channels by which nerve impulses may pass from the fibres of any excited interrupted column into those of the uninter-

rupted lateral, then the preponderance of the effect evoked by the left posterior column would show that such indirect communication between the fibres in the posterior column and those in the lateral consists chiefly of posterior column fibres, which do not cross the cord. It may indeed be doubted whether the small effects evoked by excitation of the lateral and posterior columns of the side opposite the uninterrupted lateral are any evidence of veritable crossing nerve impulses, since it is probable, that with the strength of stimulus used (2000), the excitation of any column may cause reflex discharges from the cells in the grey matter of the upper dorsal portion of the cord, and the effect transmitted by the uninterrupted lateral would therefore be due to spread of the awakened activity involving the cells which are connected with its own internuncial fibres, and which thus send forth nerve impulses to be transmitted down the uninterrupted channels.

However this may be, there is no indication by this electrical method of any large indirect crossed path, in connection with the lateral column, of fibres such as would conduct nerve impulses downwards from the dorsal to the lumbar cord. The interest which attaches to this negative result hangs upon the presumed connection of the lateral\* tract with nerve fibres on both sides, and upon the circumstance that it forms the first of a series of results all pointing conclusively in the same direction, which will be set forth in Chapters IX. and X.

(2) *Electrical Effects Evoked in the Dorsal Cord by Excitation of the Lumbar Cord, after intervening Sections.*

A. *Influence of Hemisection.*

Since the characters of the normal electrical effects in the cord are not the same when the nerve impulses are ascending, *i.e.*, evoked by excitation of the lumbar region, as when descending, *i.e.*, evoked by excitation of the dorsal region, it is not surprising that the influence of intervening lesions upon the former group of effects should differ from the influence already described upon the latter group.

The influence of hemisection upon ascending changes was studied in two animals (Cats), one with minimal, the other with maximal stimuli, the experimental tract being situated as shown in the following table, and the hemisection made on the left side at the level of the 13th dorsal and 10th–11th dorsal vertebræ respectively.

\* MIESCHER, 'Arbeiten aus dem Physiologischen Institut in Leipzig,' von C. LUDWIG; WOROSCHILOFF, *ibid.*

## INTERVENING Hemisection on the Left Side

	Cord cut for observation	Cord cut for excitation	Stimulus	Left		Right	
				Lat	Post.	Lat	Post
Cat (375)	8th dorsal	2nd lumbar	500	8	0	80	40
Cat (355)	"	"	1000	0	65	105	80
				0	26	106	86
				0	40	120	96

*"Minimal" Stimulation* — In the first Cat (375) the "minimal" stimulation in the lumbar region of the lateral and posterior columns on the side of the section evoked no appreciable effect in the dorsal region, the negative result thus confirming our previous conclusion, that the direct fibres in these columns are completely confined to one side of the cord. This, it may be pointed out, is strictly in accordance with the present state of minute anatomical knowledge, as obtained by the study of the degeneration and developmental histological changes

*Average of Effects with Maximal Stimulation* — With the maximal stimulus, no effect was evoked by the stimulation of the lateral column on the side of the interruption. This contrasts with the fact that when the nerve impulses are propagated down the cord, as in the previously described experiments, such stimulation evoked appreciable effects.

The remaining columns gave average effects of

44 for the posterior column on the side of the section,  
 110 „ lateral „ „ opposite to the section,  
 87 „ posterior on the opposite side

The posterior column thus contains indirect fibres which come into relation with cells, but through these with fibres in the column on the opposite side of the cord, and this connection is such, that apparently it offers less resistance to the passage of ascending or afferent impulses than it does to that of descending ones, or possibly special facilities exist for the discharge of cells in response to impulses ascending in the posterior column.

#### B. Influence of Section of Posterior Columns.

The influence of the section of both posterior columns upon the effect evoked by excitation of the lumbar cord was studied in the case of such lesions made upon three animals (Cats), in two of which the section was carried out at the time of experiment at the level of the 12th dorsal, whilst in the third it was done 28 days before at the level of the 10th dorsal vertebra. The results are displayed in the following table —

## SECTION of both Posterior Columns.

	Cord cut for observation	Cord cut for excitation	Stimulus	Left		Right	
				Lat.	Post	Lat	Post
Cat (256)	8th dorsal	3rd lumbar	300	30	0	45	15
Cat (197)	11th dorsal	4th lumbar	1000 max	240	65	310	105
			2000	64	35	32	25

## PREVIOUS Operation, Division of both Posterior Columns

	Cord cut for observation	Cord cut for excitation	Stimulus	Left		Right	
				Lat	Post	Lat	Post
Cat (251)*	6th dorsal	2nd lumbar	1000	68	0	30	10
			min	58	2	100	0
			max (less ether)	80	20	96	28

The differences between the results obtained from sections made at the time and beforehand, are perhaps those involved by the necessity in the latter case of using a slightly stronger stimulus. And since the different column effects are similar in both cases, the massed average of both lateral and both posterior effects evoked with the minimal and maximal stimulus respectively may be taken from all three animals.

Effect evoked by lateral columns

Minimal excitation, 55; maximal excitation, 136.

Effect evoked by posterior columns

Minimal excitation, 4, maximal excitation, 46.

It will be seen on looking at these averages, that with minimal excitation the posterior column effect practically disappears as the consequence of the interruption produced by the section; thus the view as to the localisation of both stimulus and generated impulse to these columns is true of afferent as of efferent impulses, when the former is sufficiently weak.

With a relatively more intense stimulus (or with the animal less etherised), this localisation of the effect does not occur; the excitation of the lower and posterior columns now evokes effects above the interruption, the average amount of which is as much as one-third that produced by the stimulation of the laterals, that is to say,

\* For full description of this animal as regards its condition during life and the *post mortem* appearances of the cord, see p. 439.



there are indirect fibres in the posterior columns which are not interrupted, and which connect these through cells with the lateral columns. This we have already seen in the case of the lateral column exclusion experiment (see p 398), to be also true for efferent impulses, hence each posterior column is indirectly connected with the lateral of its own side.

We now pass to the experiments made in similar preparations on one posterior column only.

*Influence of Section of one Posterior Column*—Our experiments upon this point were made on two animals, but in each case with a strength of stimulus which was not minimal, since, although in one animal the absolute intensity of the exciting currents was that generally used for minimal stimulation (500), yet the preparation was in a hyperexcitable state owing apparently to the lumbar section having hit the entrance of a posterior root. That the preparation (Cat 375) was hyperexcitable at the moment when the intervening section was to be made, is shown by the fact that with this weak intensity of stimulus the excitation of the lateral columns gave deflections of 166 and 285, and that of the posteriors of 168 and 202. We endeavoured to lower the excitability by more profound etherisation, but the results evidently belong to that class which have been considered as evoked by maximal stimuli. The true effect of minimal excitation was not, therefore, observed. The left posterior column was divided in both animals at the level of the 11th dorsal vertebra.

ELECTRICAL Effect obtained in the Dorsal Cord by Excitation of Columns in the Lumbar Region after intervening Section of the Left Posterior Column.

	Cord cut for observation at	Cord cut for excitation at	Stimulus	Left		Right.	
				Lat	Post.	Lat	Post.
Cat (375)	9th dorsal	2nd lumbar	500 max.	108	26	115	58
Cat (197)	11th dorsal	4th lumbar	2000 max	70	48	20	205

Average effect evoked by excitation of the—

- (1) Lateral columns . . . . . 78  
 (2) Posterior columns on side of lesion . . . . . 37

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The interruption in the left posterior column thus did not abolish, but only reduced, the electrical effect present in the dorsal cord above the interruption, when the column was maximally stimulated below in the lumbar region. The amount of the reduced effect is one quarter of that which can be evoked by maximal stimulation of the opposite uninterrupted posterior column. The existence of even a reduced effect is

presumably due to nerve impulses proceeding up channels which are composed of fibres starting below the section in the posterior column, but brought, by the intervention of cells, into relation with fibres contained in the lateral column of the same side, and in the posterior of the opposite side

An instructive experiment bearing upon this subject remains to be detailed. We divided the posterior roots of the 5th, 6th, 7th lumbar, and 1st and 2nd sacral nerves on the left side. After twenty-one days the animal (Cat 227)\* was used for experiments on the cord. These were of the same kind as the previous ones, the cord being divided in the dorsal and lumbar regions, and the experimental tract prepared for attachment to the galvanometric electrodes at its dorsal end and for stimulation at its lumbar. The excitatory electrical effects obtained with excitation of the different columns are given in the following table.

DIVISION of Left Posterior Roots of Sciatic Nerve.

	Cord cut for observation at	Cord cut for excitation at	Stimulus	Left		Right	
				Lat	Post	Lat	Post
Cat (227)	10th dorsal	3rd lumbar	1000	82	66	71	105
				125	71	145	205
					41		61
					30		85

Average effect obtained by exciting both lateral columns . . .

Average effect obtained by exciting posterior column on side of lesion

Average effect obtained by exciting posterior column on opposite side to lesion . . . . .

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It is clear, therefore, that the result of the division of the root was to reduce the posterior column effect on the side of the lesion, the diminution of effect amounting to about a third of what must be considered its full value, since the posterior column effect on the side opposite the lesion is probably lower than it would be in the normal animal.

If, therefore, the stimulus had been of sufficient intensity to evoke impulses transmitted by direct fibres only, then this diminution would mean that a third of these direct fibres had degenerated in consequence of the section. The stimulus, however, was evidently too strong to be classed as "minimal," and all the effects must be considered as increased by the accession of impulses proceeding up indirect paths. Hence, the experimental results suggest that from the total number of direct and indirect fibres uniting the lumbar region of the left posterior column with the dorsal

\* For full description of this animal see p 466

region, the section of the posterior roots has withdrawn from active service a proportion equivalent to about one-third and rendered them incapable of conducting impulses

It is conceivable that the cells in the posterior horn, which, in some animals,\* are in relation with the posterior root fibres, may have their functional activity impaired by the section and consequent degenerative changes, and that a small part of the diminution may be due to the withdrawal of impulses possibly generated in them (See Chapter XI)

### *C. Influence of Section of both Posterior Columns and one Lateral*

In order to ascertain to what extent ascending impulses started by lumbar excitation of the lateral column are interrupted by its section, a similar experiment to that described with descending impulses was carried out. An intervening hemisection on the left side and a further division of the posterior column on the right side were made, there remained only the lateral of one side, the contiguous grey matter, and the anterior columns to bridge across the interruption (MIESCHER).

The cord was prepared and excited as in all the previous experiments, two strengths of stimulus being used, both more than "minimal."

	Cord cut for observation at	Cord cut for excitation at	Stimulus	Left		Right	
				Lat	Post	Lat	Post
Cat (355)	8th dorsal	2nd lumbar	1000	0	0	110	19
			2000	0	19	220	40

It is evident from this experiment that (1) the excitation of the uninterrupted lateral column of the right side alone produces a marked effect; (2) that the excitation of the posterior columns can evoke effects in spite of the interruption in the lateral, (3) that effects can be obtained from the posterior column of the same side with an intensity of stimulus which is not effectual in the case of that of the opposite side, (4) that even with the strongest intensity of stimulus used, excitation of the interrupted left lateral column evokes no result. We may, therefore, infer that afferent tracts in the cord lying in one lateral column are brought into relation with the posterior but not lateral column of the other side. The importance of this result will be realised if it be remembered that it has been concluded from the result of physiological experiments (WOROSCHILOFF, &c.), to be detailed in the next chapter (p 419), that the majority of sensory fibres entering the cord pass into the lateral column of the opposite side, the remainder continuing in the lateral column of the side on which

\* See FREUD's paper on the cells in *Petromyzon*

they enter. It has been shown by the present experiments that, as far as the nerve impulses aroused by electrical excitation of nerve fibres in the cord are concerned, no such extensive crossing occurs in the dorsal or lumbar regions; and the experiments in Chapters IX and X, on the relation of the cord to the lumbar nerves, show that no such extensive crossing into the opposite lateral column occurs when the impulses are generated in the entering nerves themselves.

It is difficult to perform a satisfactory experiment on the influence of section of one lateral column, since the extensive lesion alters the excitability of the posterior column of the same side, and this interferes with the sharpness of the results. To avoid this we made the experiment upon an animal (Cat 259)\* in which thirty-four days previously the lateral column had been severed on the left side at the level of the 10th dorsal vertebra. The cord was then divided and prepared in the dorsal and lumbar regions, and the following results obtained --

	Cord cut for observation at	Cord cut for excitation at	Stimulus	Left		Right	
				Lat	Post	Lat	Post
Cat (259)	4th dorsal	1st lumbar	1000	0 Trace	40 50	38 37	40 73

Average of lateral on side of section	Trace,
Average of lateral opposite to section	37,
Average of posterior columns	51

The lateral column interruption with this intensity of stimulus, which from the inexcitable condition of the cord was practically minimal, is thus sufficient to absolutely block any transmission upwards of nerve impulses generated in those fibres of that column which lie below in the excited lumbar region.

\* In this animal, just before the experiment, it was found that there was spastic paralysis in the left hind limb with diminished sensibility. The knee jerks were equal and normally present. On microscopical examination the lesion was found to have destroyed the lateral column of the left side, the outer portion of the anterior column, and the dorsal two-fifths of the posterior column, while, on the right side, a portion of the posterior median was injured. Of descending degeneration there was noted the posterior third of the left lateral and the median portion of the left anterior column. Of ascending degeneration a section at the 5th dorsal showed degeneration in both postero-median columns, extensive on the left side, but only few fibres in the centre of the right column. Left cerebellar and antero-lateral tracts degenerated.

## SECTION 10.—SUMMARY OF RESULTS

It will be well now to express the general conclusions founded upon a comparison of all these experiments, especially those involving the influence of intervening sections upon the cord electrical effects.

I. If a portion of cord be severed by a dorsal and lumbar section from its connections above and below, then stimulation of either lateral or posterior column at one end evokes electrical effects at the other, which are dependent for their amount on the uninterrupted structural continuity of fibres in the particular column excited, and the electrical changes are thus the index of the arrival at one end, of nerve impulses generated at the other, and propagated mainly along the fibres in each column.

II If the stimulus used be minimal, then the interruption due to the section is in every case sufficient to practically abolish the effect; hence, with this stimulus, the nerve impulses aroused by localized stimulation of fibres, which are exposed in the section, are entirely confined to the particular column excited. This is true, whether the stimulus be central or peripheral to the observed region, that is, whether the impulses are ascending or descending.

III If the stimulus be maximal, then a greatly reduced effect is still obtained, in spite of the interruption. This effect is due to nerve impulses, which must at some period be conducted along indirect fibres outside the excited column. Its average amount varies in the different columns. These amounts may be arranged in series as shown in the following table, in which the nature of the excitation and of the interruption is noted, and the average effect evoked by maximal stimulation is given.

Character of impulses	Column excited	Column interrupted	Effect
Ascending	Lumbar end of cut posterior	Section of same posterior	52
		Section of both posteriors	46
		Hemisection same side	44
		Section of both posteriors and lateral of opposite side	40
		Section of same posterior	35
Descending	Dorsal end of cut posterior	Section of both posteriors and opposite lateral	32
		Hemisection same side	29
	Dorsal end of cut lateral	Hemisection same side	23
Ascending	Lumbar end of cut posterior	Section of both posteriors and lateral of same side	19
Descending	Dorsal end of cut posterior	Ditto	16
	Dorsal end of cut lateral	Section of both posteriors and lateral of same side	11
Ascending	Lumbar end of cut lateral	Hemisection same side	0
		Hemisection same side and section of posterior of opposite side	0
		Section of lateral same side	0

IV The table just given indicates that the indirect path along which impulses are conducted from the excited end is not confined to the column, and suggests that the size of the effect evoked indicates the amount of indirect connection through cells with other columns

V. The magnitude of the indirect effect evoked is greatest in the case of the lumbar excitation of the posterior columns, the afferent indirect connections leading upwards from this column are, therefore, either very numerous or offer little resistance, and spread largely into other regions

VI The effect is still comparatively large when evoked by dorsal excitation of the interrupted posterior column. There are, therefore, indirect connections leading downwards towards the periphery, possibly the same to some extent as those just mentioned in V, but either less numerous or offering more resistance, or spreading to a less extent into other regions.

VII The excitation of the dorsal end of the interrupted lateral column evokes electrical effects, hence indirect connections are thereby suggested spreading from the lateral column downwards into other regions; these, however, are less numerous or offer more resistance than those mentioned in VI.

VIII. The excitation of the lumbar end of the interrupted lateral column evokes no effect, hence all the channels in this column, by which impulses could pass upwards, are absolutely confined to the column.

IX The striking feature of the preceding conclusions is that the connections of the fibres of the posterior columns are framed on a different plan from those of the laterals. The posterior column fibres spread into other columns both as they ascend and to a less degree as they descend; the lateral fibres, however, spread into other columns particularly as they descend. The posterior columns offer thus special facilities for conveyance and distribution of afferent impulses, the lateral special facilities for the conveyance and distribution of efferent impulses

It will be remarked that the conclusions just suggested as to the relations of the columns are in accordance with the views of SCHIFF, "*die Hinterstränge bis ins Hirn hinein bilden die Legislative, die Turck'schen Bündel erwecken die Exekutive*"

In conclusion, we draw attention to the general indications as to the structure of the cord which the whole of these experiments imply.

Since the electrical effect obtained by the "minimal" stimulation of the cut end of one column is apparently due to the excitation of the direct fibres in that column only, the average amounts obtained in the case of the different columns is related to the excitability and number of the fibres contained. As regards the excitability of the direct fibres in different columns, there is no reason for supposing that these direct fibres, which have no connection with cells between the two ends of the experimental tract, are in any marked degree more excitable in one column than in another. The amount of the "minimal" effect must therefore depend upon the number of fibres



excited, and a comparison of the amounts in the two columns would thus give a rough estimate of their comparative number

In the Cat the effects up and down evoked by the minimal excitation of the posterior column are 92 and 74, that is an average of 83, those similarly evoked by minimal excitation of the lateral column are 42 and 55, giving an average of 48. Hence we infer that the direct fibres in the Cat between the dorsal and lumbar regions are nearly twice as numerous in the posterior as in the lateral columns. In the Monkey similar averages are 31 for the posterior and 75 for the lateral, hence in this animal we infer that the direct fibres are at least twice as numerous in the lateral as in the posterior column.

In both animals "minimal" excitation of the anterior columns at one end of the experimental tract evokes a doubtful effect at the other end, and we infer that there are few, if any, directly continuous fibres leading in these columns between the mid-dorsal and the lumbar regions. Indeed, the cord may be divided in its anterior region\* without in any way interfering with the production of electrical effects, either on the peripheral or central side of the division. Further, the application of more intense stimulation to the anterior columns although producing local movements evokes no constant electrical effects, the only results ever obtained being either with the use of considerable intensity of stimulation or with the animal but very slightly etherised. In these last cases, the magnitude of the local movements renders any strict localisation of the stimulus upon the deeply situated anterior columns impossible, any results obtained under such circumstances we therefore rejected as absolutely untrustworthy.

It must be borne in mind that in all the preceding experiments a degree of anæsthesia was used, with which no violent movements were caused by any of the stimuli employed. How far the relations of one column to another can be detected in the unanæsthetised animal by the employment of similar methods to those now used, does not seem to us a question likely to yield fruitful results by its attempted solution. The nervous impulses generated by the direct stimulation of fibres are undoubtedly far more intense in their character than those which form the flow of the sensory and motor processes in the normal animal. This is especially true when the fibres in the posterior roots and the cord are subjected to external stimulation, possibly because some mitigating influence of the cells in the posterior root ganglion is removed. Hence, when such external stimuli are used, it is desirable that these should be of the weakest character consistent with obtaining definite results, and that the animal should be in a state of narcosis sufficiently profound not merely to cause complete insensibility to pain, but the abolition of all violent reflex movements.

The conclusions as to the conduction of nerve impulses in the cord of the Cat and Monkey, to which the study of the foregoing experimental details has brought us, are only true when these impulses are generated in the mode hitherto employed, viz, that of

\*These experiments will be published in detail in a later communication in which we shall specially deal with the anterior columns



electrical excitation of the fibres of the cord itself. We have, however, used for the sake of control, a method which did not involve such stimulation, that, namely, of injecting a dose of a 1 per cent solution of acetate of strychnia sufficient to ensure toxic effect

Under those circumstances, whether the upper or lower end of the experimental tract is connected with the galvanometer, marked electrical changes, evidently excitatory, are produced whenever by touching the afferent nerves of the experimental tract a strychnia convulsion is evoked. Hence the impulses thus generated in the cells of the cord pass both up and down along the nerve fibres. As to the channels in which they pass, we can only say that since a section of the whole ventral or anterior portion of each half of the cord did not sensibly diminish the amount of the electrical changes, whilst a section of the whole dorsal or posterior portion of each half of the cord did notably diminish the amount, it would seem that these channels along which the discharge of the cells passes are situated in the dorsal half of the cord, that is, in the posterior or dorsal third of the lateral columns, the posterior columns, and the posterior horns

In another experiment of the same general kind, we divided the upper end of the cord into two halves, dorsal and ventral, as described in the method of operative procedure (Chapter III, Section 2.) We then connected each half with the galvanometer electrodes, and observed the amount of the electrical changes in each during strychnia spasms. The changes in the dorsal half were very much more marked than those in the ventral (anterior) half, thus not only confirming our previous conclusions that the nerve channels by which the impulses were conducted were situated in the dorsal half of the cord, but also suggesting novel considerations as to the source and direction of discharges of nerve energy in the cord (See Chapter XI)

This experiment being rather framed to control our method than to ascertain channels of discharge, must not however be considered as conclusive.

Finally, it will be noticed that we do not attempt to differentiate between the different columns of nerve fibres which are situated in the lateral column, direct cerebellar, antero-lateral, pyramidal, &c

We will now pass on to consider the electrical changes evoked in the cord, not by stimulation of its own fibres, but those of its nerves

CHAPTER IX—ON THE ELECTRICAL EFFECTS EVOKED IN THE SPINAL CORD BY  
EXCITATION OF THE LUMBAR NERVES

Section 1—Introductory

Section 2—Results of Preliminary Experiments

Section 3—Present Knowledge as to the Conduction of Afferent Impulses by the Spinal Cord

Section 4—Anatomy of the Lumbar Plexus in the Cat and Monkey

Section 5—Method involving Intervening Sections

Section 6—Influence of Hemisection

Section 7—Section of Posterior Columns

A Both Columns

B Column same side as Nerve

C Column opposite side to Nerve

D Section some time previous to observation

Section 8—Section of the Lateral Columns

Section 9—Summary of Results

## SECTION 1.—INTRODUCTORY.

The presence of excitatory processes in the bundles of nerve fibres which compose the spinal cord is characterised, as the experiments detailed in the preceding section have shown, by very definite electromotive changes. It is thus possible to extend the field of enquiry which the estimation of the amount and character of these changes has opened up, so as to embrace not merely the relations of the fibres in one portion of the cord to those in another portion, but the relations of these to the entering and issuing nerves. The importance of obtaining some definite data with reference to these questions will be obvious when it is remembered that there is hardly any subject in which the evidence is at once so conflicting and so unsatisfactory as that of the paths by which afferent and efferent impulses travel from and to their respective nerve roots. If the present method of observing the excitatory electromotive effects is a trustworthy guide to the presence and amount of nerve impulses in the particular region connected with the galvanometer or electrometer, then there is every hope that its application in experiments, designed to show the relations now referred to, will be one from which definite results may be expected. How far this is borne out the following experimental details will indicate, but it may be at once stated that the procedure has not belied its promise, and that, by applying still more accurate and delicate methods of the same kind, there is every reason to suppose that in the future results still more definite will be obtained, and that the actual differentiation of the afferent from the efferent fibres in their course through the bulbo-spinal system will thus be arrived at. In this manner another method will be secured for research into the anatomy of the central nervous system.

We must again note that there are two considerations concerning the functional causation of any excitatory process in the cord, that of pure conduction in fibres, and

that involving the activity of the corpuscles. If, then, on exciting a mixed nerve it be found that excitatory processes are present in a distant portion of the cord under investigation, these may be due to—

(1) The propagation of these processes from the point of stimulation along direct and continuous nerve fibres which pass into the cord and on through the investigated region,

(2) To the reflex discharge of interposed cells in the cord, brought about by the arrival of excitatory processes which, having travelled up the nerves from the point of stimulation, have entered upon paths ending in cells. These cells being thus awakened, themselves start nerve impulses which travel on up the cord, and, reaching the investigated area, produce the observed electrical effects,

(3) To the mixture of effects produced by impulses both in direct paths and the indirect ones just described.

It must, therefore, be borne in mind throughout the present research that these different causes may be operating in the production of the electrical effects observed, hence, one of our first experimental enquiries was to endeavour as far as possible to discriminate between the effects referable to the direct fibres actually excited, and those which were related but indirectly with these fibres, being primarily associated with channels connecting the area of investigation with corpuscular mechanisms in the cord.

This we have attempted to do by employing such a low intensity of stimulation as should in any particular degree of narcosis be sufficient to evoke nerve impulses, as evidenced by electrical changes, and, at the same time, not so intense as to arouse any sign of reflex movement. The weak impulses thus generated in the excited nerve presumably pass for the most part, if not entirely, along direct nerve fibres in the cord which are not in relation with nerve cells before arriving at the region observed (mid-dorsal), the evidence to be detailed later strengthens this presumption.

The subject matter now dealt with really comprises the whole question of the relation of the bulbo-spinal system to the lumbar nerves. It is obvious that this relationship is one which may be discussed under three heads according to the particular part of the nerve tract under observation.

First, the characters of the nerve impulses which pass along the channels of the cord after entering it by its nerve roots,

Second, the characters of the nerve impulses which, aroused by excitation of the channels of the cord and passing out into its nerve roots, descend along fibres of the mixed nerve,

Third, the characters of the nerve impulses which enter and leave the cord by virtue of its so-called central structures and their various connections.

Of these three groups, the first alone will be treated of in the present chapter, the second and third being reserved for Chapters X and XI. respectively

## SECTION 2 —GENERAL PLAN AND RESULTS OF PRELIMINARY EXPERIMENTS

The experiments to be referred to in this chapter were made upon both Monkeys and Cats, and all involved the following operative procedure. The spinal cord of the etherised animal was exposed in the lower dorsal region, it was then divided and prepared on the peripheral side of the section for 4 centims, so that the upper end of this lower fragment of cord could be raised from its canal and attached to the cables of the non-polarisable electrodes as described in the previous sections. The galvanometer circuit was then brought by one electrode into relation with the cross section of the cord, by the other with a ring of longitudinal surface at about a centimetre distance (See Plate 29)

The two sciatic nerves were now exposed and divided, so that they could be raised and the central end placed, when desired, upon a pair of platinum electrodes (see p 301 and fig 3), precautions being observed in their preparation with respect to maintenance of circulation, drying, &c, as indicated at length in Chapter III.

If the large and persistent resting electrical difference between the cross section and surface of the cord be balanced, and the galvanometer needle thus brought into its zero position, then on exciting the central end of either sciatic nerve for 5 seconds with the interrupted induction current (Helmholtz side-wire), an electrical change occurs in the cord, the surface contact becoming galvanometrically negative to the cross section.

On the cessation of the excitation, the needle rapidly returns to its original point and, in most cases, then continues to slowly move to a position upon the opposite side of the zero, thus indicating that the excitatory negative change only lasts as long as the excitation, but is succeeded by a more lasting after-effect of opposite sign. This increase in the resting difference has been already alluded to in Chapter IV. Errors due to any electrical escape are minimised by the nature of the excitation, and the position of the galvanometer electrodes (see Chapter III, Section 4), moreover convincing proof that the effect is truly an excitatory one is afforded by the following facts.—

(1) A similar negative change occurs when, with the sciatic nerve uncut, the skin over the foot is pinched with ivory or touched with a hot glass rod;

(2) A sudden change of small amount, but similar in sign, is produced when the nerve is mechanically excited by a ligature, cut, &c.;

(3.) Very pronounced effects of similar sign occur when, after injection of a few drops of a 1 per cent. solution of strychnia acetate, the nerves connected with the lower part of the cord are mechanically excited.

The electrical change in the cord is thus excitatory, and its resemblance to that in nerve warrants the presumption (see p 277) that it is due to the passage of excitatory impulses along nerve fibres present in that portion of the cord with which the galvanometer is connected.

*Etherisation.*

These nerve impulses may, as before stated, have two direct sources of origin, namely, the excited mixed nerve or the grey matter in the cord, which the arrival of afferent impulses may have thrown into functional activity. They may be conducted along direct fibres from the lumbar nerves to the dorsal cord or to central mechanisms, and from these either along continuous fibres to the area observed or along short internuncial fibres to other cellular mechanisms, and so again to others and thus finally reach the area.

That the change is due to the presence in varying degrees of all these three factors is extremely probable from anatomical considerations, since GAULE\* has shown that the number of fibres in the Frog's cord can be satisfied by such a triple arrangement. It is, moreover, clear, from the influence of profound etherisation upon the electrical change, that, when an adequate strength of stimulus is employed, the galvanometric effect varies in amount with the pronounced or slight character of the visible reflex effect. This has been already referred to (p. 372), but its importance in connection with the subject of this section warrants the introduction of some experimental details. We therefore give as examples the following.—In one case, on exciting the sciatic of a profoundly etherised animal (Cat) with a weak but adequate stimulus for 5 seconds, the galvanometric cord effect was 76 scale; the animal was then less etherised and the effect was 220 scale. On again deeply etherising the effect with the same excitation sank to 130; upon the ether being then more or less removed, the excitation produced an effect of 200, whilst on renewed profound etherisation this was only 80. In all these cases very feeble reflexes or none were observed in the profoundly etherised animal, but the reflexes were well marked when with less narcosis the larger electrical changes were noted.

These differences evidently point clearly to the fact that the electrical change may not only be that due to the transmitted nerve impulses up direct tracts, but also to the presence of interposed cellular mechanisms and their susceptibility of response to the arrival of afferent impulses. In Chapter III we have discussed the value of the use of ether as a means of discriminating between the functional activity of fibres and of fibres *plus* cells, to that chapter we refer the reader, merely remarking now that we must not lose sight of the fact that etherisation, especially when very profound, may affect the nature of the excitatory processes in the nerve fibres themselves, as in the experiments made on the nerve of the Frog by BIEDERMANN with ether vapour. The differences between effects obtained with unvarying intensity of stimulus but different degrees of narcosis are practically the same as those obtained with different strengths of excitation and unvarying but not too profound anæsthesia.

\* GAULE, 'Abhandl. Math.-Physik. Classe d. Kgl. Sachs. Gesellsch. d. Wiss.', 1889 (vol. 15, No. IX), 'Neurol. Centralblatt,' vol. 9, p. 3.

*Relation of Effect to Strength of Stimulus*

To ascertain this relationship, the practice we employed was to use an initial strength of stimulus which was just sufficient to produce a cord electrical effect when applied to either nerve with the animal efficiently narcotised, then to follow with a stimulus of double that intensity, and observe the now increased value, and finally to proceed by doubling the strength of stimulus until a point was reached when the effect was only slightly altered. Such an experiment is the following one made upon the Cat. An initial excitation for 5 seconds with the secondary coil at a distance of 500 (see Chapter III on experimental method and apparatus) gave a cord effect indicated by a galvanometric deflection of 65; similar excitation of twice the intensity, 1000, gave a cord effect of 122, and an excitation of four times the intensity, 2000, gave a cord effect of 152. In the Rhesus Monkey a similar result was observed, thus an initial excitation for 5 seconds of the sciatic nerve, with the coil at 2000, gave a cord effect of 32 (galvanometer deflection), whereas twice the intensity of stimulation, 4000, gave 60, and three times the intensity, 6000, gave 78. These selected individual examples furnish data which are strictly in accordance with the average effect as deduced from all the observed instances which occur in our experimental records. Thus if we select all the unexceptional readings of galvanometric cord effects obtained in both Cat and Monkey with the initial strength of stimulus, the average of seventeen is 56, similar readings (twelve instances) with twice this strength of stimulus give an average of 100, whilst the average of sixteen instances with four times the initial strength is 168. It is thus evident that the cord effect increases with the intensity of the stimulus at first in direct proportion to the strength, but afterwards in one less directly related with this factor. A point is ultimately reached at which no increase, but a decrease, in cord effect occurs. This, it need hardly be said, is partly dependent upon the damaging effect of the stronger exciting current upon the stimulated nerve, and partly upon the fatigue of the cord cells through the arrival in the cord of the very intense nerve impulses evoked by the strong stimulus. In these experiments, as in all others to be referred to in this section, the number and characters of the successive stimuli employed were the same in each case. (See Chapter III. Section 3.)

It is remarkable how close the amounts of the different cord readings obtained in various individuals of one species are to one another, and how often, especially in later experiments, the initial intensity of stimulus required with different nerves and different animals was the same (500 coil), thus showing the similarity of the narcosis. We may here draw attention to the minimum and maximum effect obtained in the Cat, the first with the coil at 500 and the second at 2000, the minimum being 20, the maximum 340. So far then as the relation between the size of the cord effect and the strength of the nerve stimulus is concerned, there is a strong resemblance between a nerve-to-cord excitatory electrical change and that in a nerve; the ether effect before-mentioned



indicates, however, a difference, since we have not as yet observed in the Cat or Monkey any such very marked change in the excitatory effects in purely nerve preparations as definitely dependent upon the degree of etherisation

The absolute determination of the true character of the minimal cord effect, and the question to what extent it is to be considered as entirely due to the propagation of nerve impulses along direct and continuous paths, unmixed with impulses generated in nerve centres, might be settled by accurate experimental observations upon the time relations of the cord electrical change, particularly the time of its development relation to the seat of nerve excitation. Such an enquiry would doubtless involve the use of Bernstein's differential rheotome, since the small size of the minimal effect is a serious objection to the use of the much simpler method of recording by photography the movement of the meniscus of a capillary electrometer

It may be mentioned incidentally at this point that the cord effect evoked by a single electrical excitation of the sciatic nerve was, however, sufficiently pronounced to cause a distinct movement in the mercury of our capillary electrometer. The movement when magnified 300 times was just visible with a weak stimulus (coil, 500), and was quite marked with a maximal stimulus (coil, 2000). It was always a single movement, but appeared to the eye rather more prolonged in character than that which was obtained in the case of the single nerve effect as displayed in the photographs of our former paper \*

It may be asked at this juncture upon what evidence we assume that the effect in the cord, following the excitation of the sciatic nerve, is due solely to the arrival therein of nerve impulses which have travelled up posterior or afferent fibres. The evidence, which is supplied in full detail (in Chapter XI.) upon the relations of the nerve fibres and the nerve cells, shows that no electrical changes appreciable by the galvanometer can be produced in the cord by even strong stimulation of the anterior or efferent roots

It is thus clear that stimulation of the sciatic nerve generates nerve impulses which enter the cord by the posterior roots only, although, owing to our ignorance of the influence of the spinal ganglion, it cannot be assumed that the impulses are the same in character as those generated by excitation of the posterior roots themselves. We may now pass on to the consideration of the object of our experiments

The object of the investigation will be best set forth by considering the present position of our knowledge of the relations of the spinal cord to the lumbar nerves, and particularly to the afferent fibres of those nerves. For if we are justified in assuming that the electrical effect observed in the cord is due to the passage of nerve impulses, and their arrival at the portion of the cord under observation, then, since the method of observation is one which furnishes us with quantitative data, its employment places within the experimenter's grasp a means of ascertaining to what extent these impulses can be interrupted by definite section of any one tract of cord

\* Roy. Soc. Proc., *loc. cit.*



fibres, and thus of indicating which groups of fibres in the cord form the chief channels of conveyance; and the value of this method will be manifest when the character of those previously used and the conflicting nature of their results, have been placed before the reader

### SECTION 3 — OUR PRESENT KNOWLEDGE AS TO THE CONDUCTION IN THE CORD OF AFFERENT IMPULSES

We have already referred in Chapter II to the investigations made by previous experimenters in order to determine the paths of conduction in the spinal cord. It will, however, be advantageous to select the most typical of these experiments and discuss their results, in order that the scope of these methods, together with those excellencies and deficiencies which each possesses, may be clearly in the mind of the reader, before the uses of that which we advocate and its results are entered upon.

The various methods may be grouped as anatomical and physiological

#### I *Anatomical*

The posterior root fibres have been traced into the spinal cord, and a considerable number\* (according to KOLLIKER the majority) of these have been seen to divide and send branches up and down the cord. The further course of these fibres has up to the present been traced only by the method of degeneration.

(*a.*) It has been ascertained that when, in consequence of section of a lumbar posterior root, the fibres upon its central side degenerate, the degeneration is continued in certain regions of the posterior column of the same side, such degeneration up to the present only being seen in parts above the entering root. In other words, the degenerated fibres present in the posterior root are represented in the cord above the root by certain fibres in the posterior column of the same side. These fibres are believed to be the direct continuation of some of the fibres in the root; they are situated in the postero-external column at first, but gradually shift towards the middle line as they ascend, and ultimately occupy a definite portion of the postero-median column. In addition to these fibres which appear to have a continuous course up the posterior columns of the cord, there are others which show degeneration only in the immediate neighbourhood of the entry of the root, these are situated in the posterior root zone and in the marginal zone, as well as in the postero-external column. They are characterised by only occurring in that portion of the cord which lies above the root, and by being all on the same side of the cord as the lesion. Hence these fibres, whilst in direct continuity with fibres in the root, either end (KOLLIKER)

\* GÖTTGE: 'Anat. Anzeiger,' vol. 5, pp 13, 14. RAMON-Y CAJAL 'Trabajos del Laboratorio Anatómico de la Facultad de Medicina,' Barcelona, Abril, 1890. KOLLIKER "Ueber den feineren Bau des Rückenmarks," 'Sitzungsberichte d. Würzburger Phys.-Med. Gesellschaft,' 8 März, 1890.

or come into relation with cells shortly after entering the cord, the degeneration in consequence ceasing. This cessation of degeneration is indicated by the numerical superiority of the degenerated fibres in the posterior roots over those in the posterior column, and above all the postero-median column. As far as it goes the evidence itself afforded by this method is fairly conclusive, whatever other channels there may be, undoubtedly the above-named do exist, and thus the posterior column of the same side offers a direct tract up which some nervous impulses undoubtedly not only can, but do, pass.

(b) A similar investigation applied to the cord, since it determines all the fibres in which degeneration is seen above the level of a hemisection, carries us a step further than the above method. In this not only the fibres just indicated in the posterior column degenerate, but all the through fibres from every root below on the side of the hemisection. Further, it marks out all fibres which have their nutritive or developmental centre, not in cells in the ganglion on the root, but in cells situated in the cord below the section. Such fibres now seen as degenerated above the lesion are grouped into two parts of the lateral column, the antero-lateral, and the direct cerebellar. Except that the former is much more diffuse, the degenerated fibres being scattered about among other sound ones, there is little to distinguish the character of these two groups except their situation. They both appear to have similar terminal connections, at any rate, on the cerebral side. They are both characterised by containing fibres of very variable length, many of which appear after a shorter or longer distance to again come into relation with nerve cells, so that in these the degenerative change ceases. The characteristics of these tracts are, therefore, twofold; they appear to afford not only a direct connection between certain cells in the cord (CLARKE'S column, &c) and the peduncle of the cerebellum of the same side, but also a series of internuncial connections, by means of which cells at variable distances are brought into relation with each other.

The tracts which degenerate on the peripheral side of a hemisection are foreign to the purpose of the present chapter, one, however, may be mentioned, the so-called "comma-shaped" patch in the ventral part of the postero-external column, since it is in all probability a tract of ascending fibres which are looped downwards, the degeneration corresponding with the loop.\*

As far as this evidence under (b) goes it is not so direct as that in (a). It is conclusive as showing that, if there be crossing of any of these tracts from one side of the cord to the other, such crossing must occur by means of cells, since the degenerative change does not cross. It is further conclusive in showing that there are continuous nerve fibres in these two situations. It is not conclusive as regards the physiological characteristics of the fibres, since in anatomical evidence, as in circumstantial evidence, every link of the chain must be present for the evidence to be

\* Possibly these fibres are the descending branches of the bifurcating posterior root fibres, cf especially KOLLIKER.

complete. The essential link, that of connection with the posterior roots, the fibres of which convey afferent impulses, is, however, wanting. It is, notwithstanding, highly probable that these paths (direct cerebellar and antero-lateral), are to be classed as afferent from the resemblance in extension of the degeneration to that present in the fibres of the posterior columns.

There are many considerations connected with growth, development, &c., which suggest that ascending degeneration is the characteristic of afferent, and descending degeneration of efferent tracts in the spinal cord, in other words, that the centres of growth and nutrition are also the centres of functional activity, and, therefore, in consequence of an interruption, that loss of functional activity and loss of nutrition both occur in the part on the distal side of the breakdown. The fact, however, that the cells in the ganglion on the posterior root exercise this nutritive function on the nerve fibres on both sides, although explicable in consequence of developmental relations (His) must cause some hesitation as to the propriety of accepting, without reserve, the principle that the direction of the degeneration coincides with the direction of the function. What has happened in the development of the posterior root fibres may possibly have also occurred in the case of some fibres in the cord. Moreover, it is conceivable that even with this relation between nutrition and function, ascending degenerative changes might occur in fibres which ought to be classed as outgoing, since they would lie as much on the efferent side of the central nervous system as do those of the pyramidal tract. Such fibres would be long internuncial fibres, connecting the kinæsthetic system of the lower (lumbar) centres with the efferent side of a similar system of the upper (or cervical) region. It is conceivable that such long internuncial fibres exist, and, if so, then impulses which subsequently become motor are conveyed by them. These impulses, although afferent in the sense that they are actually travelling up the cord, are analogous in character with all the motor or outgoing impulses, since they occupy that relation to the centres from which they started.

Without insisting on these hypothetical fibres, we may again point out that the anatomical evidence becomes vague when some of the links in the chain are wanting, hence all conclusions founded upon it must be used with the greatest caution. The facts which it surely evidences are—

1. That there are continuous fibres in the cord
2. That these fibres do not cross from one side of the cord to the other
3. That a small proportion of those situated in the posterior column are in direct connection with those entering the cord by the posterior roots

## II. *Physiological.*

If we turn now to the method of physiological experiment, there is hardly any subject in the whole realm of physiology upon which such divergence of experimental

result and interpretation exists as that of the relations between the columns of the cord and the passage of afferent impulses

The contradictory facts set forth in the various papers on this subject are sufficient to justify the belief that many of the experiments made must have involved the presence of some factor of capricious character and uncertain action, common to most of them, and that the conclusions which the various experimentalists have drawn from their results are all vitiated by its presence

When such a fundamental matter as that of the extent to which the afferent path lies on one or the other side of the cord is answered so differently that, according to one set of investigators (BROWN-SÉQUARD, FERRIER, &c), it is wholly crossed, according to others chiefly crossed (WOROSCHILOFF, MIESCHER, &c), equally uncrossed and crossed (VAN DEEN, STILLING, &c), chiefly uncrossed (VON BEZOLD, MOTT), wholly uncrossed (CHAUVEAU), it is plain that the method adopted is at fault and is quite inefficient for the purpose of determining the extent to which particular tracts in the cord are concerned with the passage of impulses. The reason why the different results of former investigators are so conflicting may, we think, be gathered by the careful study of the experimental method in two of the most elaborate of the series of investigations just referred to, those, namely, carried out in LUDWIG'S Laboratory by MIESCHER\* and WOROSCHILOFF†

Although the experiments are well known to physiologists, we think it necessary to allude in a little detail to their character. Both sets of experiments were carried out on Rabbits, and in both the method consisted in the production of an intervening localized destruction of a portion of the spinal cord, and in then ascertaining what changes this destruction produced in the reaction of some more central portion of the nervous system of the animal to the stimulation of the afferent nerves of the distal portion. The reaction observed was, however, different in the two cases, it being in MIESCHER'S experiment the rise of blood pressure due to the activity of the so-called vaso-motor centre of the medulla being awakened, in WOROSCHILOFF'S, the movement of the upper limbs of the animal, due, as he believed, to the awakening of a convulsive centre in the medulla. The index used by MIESCHER being the amount of blood pressure, had the great advantage that it varied with the strength and duration of the afferent stimulation, and thus a quantitative comparison between the results of two series of stimuli was possible, and it is, perhaps, due to this that the facts have been held as affording data of so cogent a character. They show first that the reaction of the centre, as indicated by rise of pressure, is very largely reduced when the lateral column on the opposite side of the cord to that of the excited sciatic nerves has been divided; and second, that when a complete intervening division of the cord, with the exception of one lateral column, is made, the reaction still persists, being most marked when the distal nerve on the side of the complete section is

\* 'Ber d Sachs Ges d Wiss, Math-Physik Cl,' 1870. Also 'Arbeiten a d Phys Lab,' Leipzig

† 'Ber d Sachs Ges d Wiss, Math-Physik Cl,' vol 26, 1874.

stimulated. From this it was concluded that the spinal path for those afferent nerve impulses which, proceeding up one sciatic nerve into the cord, subsequently reached the vaso-motor centre, was chiefly contained in the lateral column of the side of the cord opposite the nerve. The experiments of WOROSCHILOFF extended these, and showed that movements of the upper limbs could be only aroused in response to stimulation of the skin of the lower limbs, provided that the lateral columns were intact, that destruction of the continuity of other portions of the cord did not notably influence the reaction, that when one lateral column was divided, the skin stimulation on the side of the lesion produced a greater reaction than that on the side opposite the lesion, and that when the whole cord, with the exception of one lateral column, was divided, the stimulation of the skin on the side of the intact column, produced a much less reaction than did that of the skin on the opposite side. From this last experiment, WOROSCHILOFF assumed that, since the impulses were transmitted from the lower to the upper portion of the cord by the bridge of fibres in the intact lateral column, they travelled throughout along such fibres in one continuous path, keeping entirely to the lateral column. The difficulties involved in this assumption, and the unsatisfactory character of the experiments, are ably set forth in a recent edition of FOSTER'S physiology, to which the reader is referred.\* The conclusions, therefore, to which WOROSCHILOFF arrived were that afferent impulses were transmitted entirely by fibres contained in the lateral columns, and that by far the chief part were transmitted by the fibres in the lateral column on the opposite side to the entering nerve. By his first conclusion, he therefore placed both the posterior columns and grey matter out of court, although the former must convey at any rate some impulses since they contain a considerable number of the posterior root fibres, whilst there being no means for the impulses to cross over from the entering roots to the lateral columns of the opposite side, except through the grey matter, this latter is assumed to be in operation by the second conclusion.

Apart from the contradictions involved in this interpretation of these two sets of experiments, the results remain as definite phenomena. In seeking to ascertain their true meaning, it is essential to realize all the conditions of the experimental procedure. Now, of all these conditions, the one which is the most important is that connected with the experimental necessity of evoking definite reactions.

These reactions, whether of vaso-motor, convulsive, or other centres, are profoundly influenced by anæsthesia. It is certain that in the unanæsthetised animal the centres are largely affected by the functional discharge of other centres, and that this influence, although by no means abolished, is diminished by narcosis. In all the experiments of MIESCHER and WOROSCHILOFF no complete anæsthetic was employed, the animals being in MIESCHER'S investigations simply curarised, and in WOROSCHILOFF'S fixed in a suitable holder.

\* M. FOSTER, 'Text-book of Physiology' vol. 3 p 189. Also 'Arbeiten a d Physiol Inst,' Leipzig, 1874.

This being the case, the whole series of experiments are in reality a demonstration of the extent to which one complicated reflex act is influenced by the awakening in the entire nervous system of a whole series of reflex discharges. The uncertainty which must attend such a method may be illustrated by the following experience of ourselves. It often happened in the experiments described in this paper (all of which were performed under an anæsthetic), that after not merely complete section, but absolute removal of a piece of cord 1 centim. long in the mid-dorsal region of the Cat or Monkey, mechanical irritation of the sciatic nerve, and especially of the posterior roots, caused not merely movement in the upper limbs, but of the head, &c., also. This effect was an indication that the anæsthesia had become too slight, and it was immediately abolished on making the latter rather more profound. We convinced ourselves that the mechanism of its causation consisted in first a reflex of the lower limbs, and that this movement dragging on the trunk aroused a reflex in the upper limbs by pulling on the nerves of the upper fragment of cord, which in the neighbourhood of the section was in a hyperexcitable state. The afferent impulses thus started now evoked general movements by discharging the higher centres. The movements of the lower and upper limbs often followed one another so rapidly that the eye was unable to distinguish between their time of commencement, in some cases, however, particularly when the narcosis was increased, the delay between the two was quite plain, and every stage might be observed. Of what value, therefore, as regards the question of conduction in the continuous tracts of fibres in the spinal cord are the results of experiments in which the animal is under no anæsthetic at all, for the employment of curare by MIESCHER did not provide for the adequate exclusion of reflex centres such as can be obtained by the use of ether. Indeed, MIESCHER's method depended upon the maintenance of the functional activity of the reflexes. It seems to us, therefore, that this is the crucial point of the whole position, and accounts for the capricious character of the results of different observers as dependent upon different methods of investigation. The index for the arrival of nerve impulses from one side of a block in the cord to the other has always been a reflex one, and it is essential for its proper working that the reflex centres should be in an excitable condition. Since the experiments involve operating on the cord and the examination of the animal in the unanæsthetised state, within a short time of the operation there is every opportunity for abnormal conditions of the other centres (in consequence of the procedure), to influence the result; such influence is so certain from the state of the animal that the results really determine, not the localisation of afferent fibres in the cord, but the extent to which the operation has augmented or depressed the excitability of the successive central mechanisms, and the bridge by means of which the lower and upper parts of the cord communicate thus becomes chiefly a column of internuncial fibres. Moreover, almost all experiments done within a few hours of the time of operation lay themselves open to our further criticism, that it is possible for the reflex movement of the hind limbs and trunk to arouse by mechanical pull of the parts



around the seat of lesion, similar movements of the upper limbs. That such reflex movements were present in the case of WOROSCHILOFF'S own experiments, is evident from the study of the account of those evoked in the animal after the operation had been made upon the cord. Thus, in one of his experiments (VI), the animal (Rabbit), was subjected to an operation involving the division of the spinal cord in the dorsal region, the whole cord being cut through with the exception of the lateral tract of the left side. On examining the animal an hour or two afterwards, the right hind limb was found to be paralyzed, due to section of its efferent spinal tract, this efferent paralysis being confirmed subsequently by dividing the cord below the medulla and stimulating its distal cut section when only the left hind limb responded, notwithstanding this, pressure on either foot caused movements in both hind legs. Now in this case the movement of the right leg must obviously be a reflex effect, having its central physiological seat in the lower fragment of the cord, and any arguments based upon the amount of movement of the respective limbs, must deal with the question as to the extent to which the section has heightened or depressed the normal excitability of the reflex centres in this lower fragment. But it is precisely this question which it seems to us has not been sufficiently dealt with in the text, there being a tendency to treat the cord in an unanæsthetised animal as if one of its main physiological characteristics, reflex excitability, were in abeyance in the distal, though not in the proximal and central portions. The evidence cannot, therefore, be considered as adequate to warrant his statement "Meine bis dahin voorgelegten Beobachtungen bestätigen und erweitern die Angaben von MIESCHER, NAWROCKI und DITTMAR, denn von nun an sind wir darauf hingewiesen, die Bahn, welche das Gehirn mit allen Nervenwurzeln verbindet, in dem Seitenstrange zu suchen."

The criticism just advanced is not a new one since it forms the basis of the objections of CHAUVEAU, SCHIFF, and others. Its cogency is increased by the discovery made by FODERA of hyperæsthesia after section. The most important points in connection with this for our present purpose are those brought out by experiments made by SCHIFF\* before the observations just referred to. These were, that in many cases of hemisection of the cord there is not merely hyperæsthesia below the lesion on the side of the section, but heightened reflex excitability of the cord in the neighbourhood of the lesion both above and below. This hyperexcitability is less marked when the whole cord is divided, than when a bridge joins the parts above and below the lesion. It has been found by MARTINOTT† that the hyperæsthesia is particularly bound up with injury of a particular region in the lateral column, and it is attributed by him not to a direct increase in excitability, but to the removal of inhibitory, *i.e.*, depressant, influences by the section. It may be pointed out that, as regards the nerve trunk, the experiments of HERING show conclusively that the increase of

\* SCHIFF, 'Lehrbuch d. Physiol.', 1859.

† MARTINOTT, "Hyperæsthesie nach Verletzung des Halsmarkes," 'Archiv f. Anat. und Physiol.' (Physiol. Abth.), 1890.



excitability therein caused is in direct causal relation with the electrotonic effects of the resting or persistent nerve currents produced between the cross section and the surface of the nerve trunk. Since similar electrotonic alterations in excitability have been shown to exist in the case of the spinal cord, it is most probable that a direct increase would be produced by the very large resting currents which (see Chapter IV) have been found by us to be produced by cross sections of the cord. In this connection we may draw attention to the following striking phenomenon described by SCHIFF,\* and which in the progress of the present research we have had the opportunity of seeing ourselves. We often saw that after complete section of the cord and the removal of a piece 1 centim in length in the region of the 8th dorsal vertebra, when the animal was asphyxiated on the completion of the investigation, a sudden prolonged discharge of the nerve centres in the lower portion of the cord occurred. This revealed itself by the rising up of the tail of the animal, and its maintenance in an erect position for one or two minutes. The discharge and its effect then subside to be followed in two or three minutes by a second feebler one, and this by a third still more feeble. In addition to this it often happened that during an experiment on such a preparation, rhythmical discharges of the centres in the lower portion of the cord occurred after the section, evidenced by rhythmical contractions of the anal muscles. This has also been noticed by several investigators.

Further, in one animal (Cat 325) in which the cord was divided at the 13th dorsal vertebra, although the tail phenomenon did not spontaneously appear, when the animal was asphyxiated, it was readily evoked in full strength by slight stimulation of the skin of the tail.

These phenomena afford a striking instance both of the hyperexcitable state of the centres in the lower portion of the cord and of the capacity of these centres to discharge such a series of nerve-impulses as will produce sustained co-ordinated movements.

The difficulties thus involved in the experimental methods of MIESCHER and WOROSCHILOFF are to a great extent obviated by experiments in which, a given lesion of the cord having been made with all due antiseptic precautions, the wound has been allowed to heal, and the animal examined carefully at varying intervals, from a few days to weeks and months, after the operation. Such an experiment is that made by FERRIER† on the Monkey, in which a hemisection at the level of the 8th dorsal was followed by complete insensibility below, on the side opposite the lesion, to every form of sensory stimulus, whilst the sensibility on the same side remained unimpaired. This experiment is similar to the paralysis on the same side, and anæsthesia on the opposite side, observed in some cases of injury or disease localised in one half of the spinal cord. Other observers, notably MOTT,‡ have, however, obtained results which

\* SCHIFF, PFLUGER'S 'Archiv,' vol 30, 1883, p 202

† FERRIER, 'Brain,' 1884

‡ 'Proceedings of the Physiological Society.' 'Proceedings of the Royal Society.'

vary between partial accordance and complete opposition to the above. It is not our object to endeavour to reconcile this apparently conflicting evidence, but we may point out that great difficulties are involved in the application of the tests necessary to determine the sensibility of animals. In our own experiments, which have been made upon Cats, and which involved hemisection of the cord the application of the water and other tests to the skin indicated that the afferent stimulus was conveyed from both hind legs up the cord, but with much greater certainty, and, judging by the quickness in the evoked movement, with much greater intensity, on the uninjured side than on that corresponding with the lesion.

It is evident that the flaw in all these methods is the fact that, owing to the index of the arrival of impulses above the lesion being some movement, the central structures of the nervous system must be sufficiently excitable to be capable of responding, and the stimulus used must be intense enough to arouse discharges of sufficient magnitude to evoke definite muscular movements.

Whilst the same flaw in the classical experiment is also present in the case of efferent tracts, its presence here does not produce such a blurring of the result, since the method can always be checked by a concluding experiment involving division of the cord below the medulla, and excitation of its distal portion, with observation of the amount and character of the movements of the lower limbs. Although acknowledging to the utmost the value and precision of the experiments carried out in LUDWIG'S laboratory, we must express our conviction that, as regards the conduction of afferent impulses, they do not warrant the inference either that the lateral columns contain the fibres of the afferent tract to the exclusion of the grey matter and the other columns, or that the fibres which they do contain form a continuous afferent path, it being quite possible that those fibres which undoubtedly conducted at the point of section were merely acting as internuncial links between distal and proximal portions of the grey matter. This latter was, by the exigencies of the method of observation, often, if not always, thrown into a state of abnormal excitability, and in the neighbourhood of the section this state was that of hyperexcitability.

It will be gathered from what has been said that the question of the relations of the fibres in the cord to the posterior roots can, in our opinion, only be arrived at by the use of a method which allows of discrimination between events taking place in the cord itself when, by means of complete anæsthesia, the activity of the reflex mechanisms is subdued. Such a method is that of ascertaining the electromotive changes in a portion of cord following stimulation of the afferent nerves, since the animal may be so profoundly anæsthetised as to give little or no reflex muscular contraction, and yet distinct effects can be detected in the cord. It is because the conclusions to be drawn from our results clash so markedly with those of MIESCHER, WOROSCHILOFF, &c, that we have thought it necessary to preface their introduction into this section by this detailed criticism. This divergence in the conclusions and the importance of the effective application of a method which besides the above advan-

tages has the greater one of furnishing us with the results of cord changes expressed quantitatively, and, therefore, capable of strict comparison with one another, have combined to cause us to devote a very large proportion of our experimental investigations to the subject of the present and the succeeding chapters. The subject matter of the present chapter becomes, therefore, an answer to the question, to what extent are the electrical changes in the cord, and hence the nerve impulses, of which these are the index, interrupted when between the stimulated nerve and the observed region of the cord different intervening localised sections are made. The principle is, therefore, that of the experiments carried out in LUDWIG'S laboratory, it is the index alone which is novel.

#### SECTION 4 —ANATOMICAL RELATIONS OF THE LUMBAR NERVE

Since in all the experiments which bear upon the relations of the spinal cord to its nerves the sciatic was chosen, it is desirable at this stage to refer to the anatomical relations which exist between this and the roots of the lumbar and sacral nerves.

These differ in the two sets of animals used, Cat and Rhesus Monkey, and as we are unable to find that the comparison of their anatomical and physiological relations has been anywhere\* set forth, we must proceed to examine the case of each species of animal in a little detail.

In the Cat the photograph of the plexus (Plate 35) shows that of the two branches of the sciatic nerve (*I.P.* and *E.P.*), internal and external popliteal, the former derives most of its fibres from the 6th, the latter from the 7th lumbar roots. Since the portion of sciatic nerve which we used was that in the thigh, the fibres involved were almost entirely those derived from the 6th and 7th lumbar roots, a few fibres coming from the 1st sacral, and still fewer from the 5th lumbar. The obturator nerve derives its fibres from branches of the 5th and 6th lumbar nerves, the anterior crural mainly from the 5th, but to some slight extent from the 4th.

In the Monkey the relations are somewhat different, as will be seen by referring to the photograph of the lumbar plexus of the *Macacus rhesus* (Plate 34). It will be then found that the two branches of the sciatic nerve (*I.P.* and *E.P.*) derive their fibres from a more widespread origin. The majority of fibres come from the 5th, 6th, and 7th lumbar, a few fibres from the 1st sacral join to form the trunk of the nerve, but these appear to pass entirely into that branch which leaves the trunk high up and supplies the hamstring muscles (*Hs.*). The obturator nerve derives the majority of its fibres from the 4th lumbar, receiving a few fibres also from the 5th, whilst the anterior crural derives its fibres from the 4th, 3rd, and (?) 2nd in decreasing amount.

Roughly speaking, therefore, the relations of the lumbar plexus in the two species of animals differ in this respect, that with the same number of lumbar nerves (7) the

\* While this is passing through the press a very valuable paper, giving the anatomy of the plexus in the Cat, has appeared, viz, LANGLEY, 'Journal of Physiology,' vol 12, No 4, 1891.

main supply of each nerve is, in the case of the Cat, one root lower than in that of the Monkey

The physiological connections of the roots were of importance to us only as far as the fibres in the sciatic nerve were concerned. In attempting to ascertain these connections it occurred to us that the electrical method would furnish a valuable means of ascertaining to what extent the fibres in any nerve trunk are derived from particular roots, whether anterior or posterior. All that is necessary for the carrying out of such investigation upon the sciatic nerve is to expose the cauda equina of an anæsthetised animal, then to prepare the nerve, divide it, and connect its isolated central end with the galvanometer. The various roots of the lower lumbar nerves are now divided at their termination in the spinal cord, and their peripheral ends excited with the interrupted induction current for a given time (5 seconds). If electrical effects are evoked in the central end of the divided sciatic, then, obviously, the root excited contains nerve fibres which pass down the nerve as far as the region observed. With the animal in a state of uniform narcosis, the comparative amounts of the deflection produced by applying to the different roots a stimulus of unvarying intensity and duration indicate the relative amount of fibres, provided that the excitability of the various roots is approximately the same. In this way we ascertained that the effect evoked in the popliteal region by exciting the peripheral ends of the cut anterior or posterior roots of the 1st sacral nerve was, in the Cat, comparatively small, being only one-sixth of that evoked by exciting those of the 7th or 6th lumbar, whilst excitation of the 5th and 4th lumbar was followed in the Cat by very little effect at all in the nerve. Physiological experiment thus bears out the anatomical details displayed by dissection. One obvious use of the method which the few experiments which we have carried out on this line suggests is, that it not only secures an analysis of the different fibres which pass from a complicated plexus into a nerve, but places within the experimenter's grasp a method of determining to what extent the relations of the afferent fibres of a nerve with the nerve roots are similar to those of the efferent fibres.

We will now turn to our experimental results made upon the cord itself.

#### SECTION 5.—THE OPERATIVE PROCEDURE INVOLVED IN THE METHOD OF SECTIONS INTERVENING BETWEEN THE OBSERVED CORD AND THE EXCITED NERVES

\* The experiments were made upon twenty-two Cats and three Monkeys, and were all conducted in the following way. The cord of the anæsthetised animal was exposed and divided in the lower dorsal region, the particular locality varying from the levels of the 8th to that of the 11th dorsal vertebræ. It was then prepared for 4 centims. on the distal side of the section and connected at its cut and longitudinal surface with the non-polarisable electrodes by cables, in the same manner as that already described (See Chapter III., Section 3.) The sciatic nerve was then exposed, freed for some distance, ligatured, and divided. It was left in the muscles

in order to avoid cooling, &c, and only taken out of its muscular bed for purposes of excitation. The large resting electromotive difference between the surface and cross section of the cord having been balanced, an excitatory electrical effect in the opposite direction to the difference was observed to accompany the stimulation of the nerve. The amount of this effect, as indicated by the amount of the galvanometric excursion, varied, as previously stated, not merely with the intensity and the duration of the stimulus, but with the condition of anæsthesia, &c, of the animal. If care be taken to keep these factors as far as possible unchanged, the excitatory electrical effect thus produced at each repetition of the experiment keeps very fairly uniform, as much so in point of fact as in similar experiments upon Mammalian nerve trunks. When we had thus obtained a constant effect in the cord, an intervening section was made in the lower dorsal or upper lumbar region by the method described in Chapter III., Section 2. Its position coincided, in some cases, with the lowest portion of the part of the dorsal cord exposed for connection with the galvanometric electrodes, in the majority of cases with a still lower level obtained by a fresh exposure of a small portion of cord. It was found that it was not desirable to make this second exposure when the cord was first prepared, since during the time lost in the preliminary experiment, &c, the intervening cord at this point is apt to suffer.

The intervening section having been thus made, the nerve was excited under precisely the same conditions as before, and the alteration, if any, in the amount of the cord effect noted. In all such experiments the extent of the section of the cord, and thus the part involved in the interruption, is capable of great variation, and the results may with advantage be grouped in relation to the particular regions which have been involved in it, thus following the exact and strictly logical method which, under LUDWIG'S guidance, was such a characteristic feature in WOROSCHILOFF'S treatise.

#### SECTION 6.—THE INFLUENCE OF HEMISECTION.

The results of a hemisection made between the portion investigated and the entry of the stimulated nerve as regards its influence upon the electrical changes in the cord, which are evoked by the nerve stimulation, will be best seen by a glance at the subjoined table, which gives the result of the comparative observations made in the manner previously indicated in two animals before and after the section. The animal was in all cases carefully anæsthetised and kept well under the influence of the anæsthetic; the stimulus was always in any two comparative results adjusted to the same degree of intensity, and was of the same duration, whilst, as far as possible, errors due to variations incidental to the application of the stimulus, the condition of the animal, and the galvanometric condition of the observed region of the cord, were excluded, and observations in which contemporaneous changes in either of these three conditions could be detected were rejected.

*Result of Hemisection.*

## EXCITATION on same side as Section

	Deflection	
	Before	After
Cat (a) (349)	185	29
Cat (b) (327)	105	45
	132	24
Total	422	98
Ratio	100 to 23	

## EXCITATION on opposite side to Section

	Deflection	
	Before	After
Cat (a) (349)	182	165
Cat (b) (327)	82	90
	142	91
Total	406	346
Ratio	100 to 85	

In Cat (a) the cord was divided and prepared at the lower border of the 9th dorsal vertebra, and the section made at the 13th dorsal. In Cat (b) the cord was divided and prepared at the 9th dorsal. Both sciatic nerves were prepared, and first one and then the other excited in the manner previously described. The stimulus was in the above cases that of the Helmholtz side-wire, 100 stimuli per second, continued for 5 seconds with an intensity just sufficient to evoke slight reflex effects in the lower part of the cord, *i.e.*, the secondary coil was placed at 500 or 1000. The ratio of the sum of the two different columns indicates that an intervening hemisection, when on the same side as the excited nerve, will diminish the cord effect 77 per cent., and that when it is on the opposite side it also diminishes the effect, but to a very much less extent, namely, only 15 per cent.

As far then as the nerve-to-cord effect is concerned, its production is very largely dependent upon the unbroken integrity of the fibres and grey matter along that side of the spinal cord with which the stimulated nerve is connected.



It is thus clear that in the etherised animal the excitatory electrical change is conducted along the structures on the same side of the cord as the excited nerve, and if the effect is a true indication of the passage of nerve impulses along nerve fibres in that portion of the cord connected with the galvanometer, then these nerve impulses themselves must be for the most part confined to that side of the cord which they enter. Further, if we assume that the readings furnish us with data for a quantitative comparison of the amounts of the variously awakened physiological activities on the two sides of the cord, and thus of the number or intensity of the afferent nerve impulses, then this preliminary set of observations would seem to indicate that from four to five times as great a volume of excitatory change flows up the cord on the side of entry of the nerves as on the other.

This result is fully in accordance with the anatomical evidence previously referred to, and with the results of spread obtained in the cord by excitation of its own columns detailed in Chapter VIII. It is in absolute opposition with the before mentioned results of MIESCHER and WOROSCHILOFF.

The indications of these experiments are confirmed by a large amount of collateral evidence dependent upon the influence of section of the various columns. This will be seen as we detail in succession the results of our different lesions.

#### *Previous Hemisection*

In order to ascertain whether this loss on the side of the lesion was independent of all functional changes due to the shock of the operation, &c., the hemisection was made, in two instances, a considerable time (thirty days and more) before the experimental investigation.

On the first animal, Cat (283), the hemisection had been made four months previously at the level of the 12th dorsal vertebra on the left side. Before commencing the experiment the animal was carefully examined both in its normal condition and under an anæsthetic. The left hind limb was dragged in walking, and showed marked loss of muscular power. On allowing the feet to touch cold water movements were started, the right hind leg being smartly drawn up, the left only after a considerable delay. This and other tests applied to each foot indicated no impairment of sensibility on the right side (that opposite to the lesion), but considerable impairment of both tactile sensation and movements on the left, the same side. On placing the animal under an anæsthetic the left knee jerk was seen to be much exaggerated, and it was possible to start clonic spasms in this limb.

For the actual experiment the cord was divided at the level of the 7th dorsal vertebra and the upper end of the lower fragment prepared for connection with the galvanometric electrodes. The electrical effect produced by exciting each of the two prepared sciatic nerves was now observed, the stimulus used being of minimal and maximal intensity respectively and consisting of the usual series of induction currents, 100 per second for 5 seconds.



## SECONDARY Coil 500 (minimal)

	Excitation of right nerve Side opposite lesion	Excitation of left nerve Side of lesion
Cord effect	90	20
	90	28
	95	45
	Average 92	Average 31

The electrical change is thus three times as large when evoked by stimulation of the nerve on the side opposite to the lesion, that is, the right side, as on the side (left) of the division. Hence, the major part of the change must be cut off on the left side by the lesion,\* that is to say, the nerve impulses, of which the change is an index, are unable to ascend the cord on the left side to the observed region in the neighbourhood of the 7th dorsal, owing to the hemisection at the 13th dorsal interrupting their path. If we suppose that the actual effect observed by stimulating the left nerve is due to impulses which normally cross the cord, whilst that observed by stimulating the right is due to impulses which do not cross, then the interruption has cut down the effect which the normal excitation of the left sciatic nerve would produce from  $92 + 31 = 123$  to 31, i.e., 75 per cent.

When the stimulus was four times the intensity of the above, that is, sufficient to evoke strong reflex contractions, a similar disproportion was found to exist although it was not so marked.

This is shown by the following table —

## SECONDARY Coil 2000

Excitation of right nerve	Excitation of the left nerve
340	170
215	160
220	135
Average 258	Average 155

\* In this animal microscopical examination of the cord showed that the lesion involved all the left lateral and posterior columns, the whole grey matter, and, except its median edge, the anterior column. Of ascending degeneration there was beautifully marked destruction of the left postero-median column, as also of the direct cerebellar and antero-lateral tracts, and a few degenerated fibres in the right postero-median column. Of descending degeneration there was, immediately below the lesion, degeneration in the left lateral pyramidal tract and also in left the anterior column.

The effect even with this strong stimulus is nearly twice as large when evoked by the nerve opposite to the side of the lesion. Since, however, a considerable effect is evoked by stimulation of the nerve on the same side, the use of the stronger stimulus has either produced more impulses strong enough to cross the cord, or it has caused a more complete discharge of the central mechanisms in the grey matter.

The other animal, Cat (259), had a section made upon it at the 10th dorsal vertebra thirty days before the observations were to be made. The section involved the left lateral and the majority of the left posterior column. The subsequent examination of the cord showed that the section involved on the left side the lateral column, the ventral portion of the anterior column of the grey matter, and the dorsal half of the posterior column, on the right side the posterior median column. The ascending degenerative changes were at the 5th dorsal traceable on the left side to a marked degree in the direct cerebellar and antero-lateral tracts, and in the posterior root zone and posterior median columns. A much less extensive degeneration was found to have occurred in the posterior median column of the right side.

The animal, when examined before the experimental observations, showed spastic paralysis of the left hind limb, and marked diminution in the tactile sensibility of both hind limb and trunk on the left side. The knee jerks were equally present on the two sides. The experimental investigation, as far as it relates to the present question, involved the section of the cord at the 4th dorsal (this was accompanied by prolonged tetanus of lower limb muscles and those of the tail), the preparation of the upper end of the lower fragment and the excitation of the two sciatic nerves. The excitation of the right nerve evoked effects of 43 and 56, the left of 15 and 22. The sum of these readings is 99 for the right, and 37 for the left side. If, as in the previous experiment, we suppose that the total sum of the two effects roughly represents the full responsive change of either nerve excitation, then the effect on the side of the chief lesion (hemisection) is reduced from that in the ratio of 136 to 37, *i e.*, 100 to 27, that is, it has been reduced 73 per cent. through the hemisection.

The result of these experiments is to show that the excitatory changes in the cord, evoked by stimulation of the sciatic, are largely limited to the same half of the cord as the excited nerve, the amount of limitation being such that three times the effect, and presumably three times the number of nerve impulses, proceed up the cord on the side of entry than that which is evoked by impulses either crossing in the cord, or freshly generated by cells in response to the arrival of impulses in the grey matter on the opposite side.

Our method, however, enables us to determine not merely that the excitatory effects in the cord are to a great extent limited to the side of the entering nerves, but also that the effects are mainly dependent upon the unbroken integrity of particular columns of fibres on this side. To observations on this point we now pass.

## SECTION 7 —THE INFLUENCE OF SECTION OF BOTH POSTERIOR COLUMNS

*A Section of both Posterior Columns*

The anatomical evidence clearly shows that there is an unbroken path between some of the entering afferent fibres and the fibres in the posterior column, and that these subsequently pass more or less completely into the posterior median column from the posterior root zone. It was therefore essential to ascertain to what extent the cord effect was dependent upon the presence of these fibres. This we have endeavoured to do by first ascertaining to what extent the effect is due to the unbroken integrity of both posterior columns. A remarkable incident in the course of our experiments led us early to suspect that by far the greatest part of the effect, whether crossed or direct, is conducted along these tracts. In the course of the operation for one experiment, whilst opening up the neural canal, the point of the bone forceps slipped, and so slightly bruised the posterior columns that the injury could not be detected at the time. The preparation was proceeded with, and the cord divided at the 8th dorsal. The upper end of the lower fragment was then connected in the usual manner with the galvanometric electrodes, and the sciatic nerves exposed for excitation. Only extremely small cord effects were, however, evoked by the excitation. We then discovered the bruise and determined to make a fresh section below the injury, exposing for this purpose more cord, on connecting this fresh portion with the galvanometric electrodes and exciting the nerve, an effect of 175 scale was obtained.

We now made a direct experiment along the lines thus indicated.

The cord was exposed in a Cat, and divided at the 10th dorsal vertebra, prepared for 4 centims. and connected with the electrodes by its surface and cross section. Excitation of the left sciatic nerve, with the secondary coil at 2000 (1 Daniell in primary) for 5 seconds (500 stimuli), produced cord effects indicated by a deflection of 75 scale. The posterior columns were then divided at the level of the upper border of the 12th dorsal vertebra, and a similar excitation was accompanied by a deflection of only 12 scale. As a control, the cord was now completely divided at this latter level, and the part distant from the new section was connected with the galvanometer, when a similar excitation produced a deflection in one case of 64, in another of 75 scale, thus indicating that the great diminution of the effect was due to the local operative interference with the posterior columns, and not to any general alteration in the condition of the whole cord.

A similar result was obtained in another animal (Cat), in which the cord was prepared and connected with the galvanometer at the level of the 10th dorsal vertebra, and the cauda equina having been exposed, the central end of a cut posterior root was excited, instead of the sciatic nerve. In this case the cord effect,

which was accompanied by reflex movements, was 210 with the columns intact, and after their division at the level of the 12th dorsal vertebra, sank to 36

In the Monkey this marked diminution was also found. Thus in a *Rhesus* the cord was divided at the lower border of the 6th dorsal vertebra, and prepared as before. Excitation of the right sciatic nerve evoked a cord effect of 82, excitation of the left sciatic an effect of 60, after division of both posterior columns at the level of the lower border of the 11th dorsal vertebra, excitation of the right sciatic produced an effect of only 18, and that of the left sciatic an effect so small as to be indicated by a mere trace, viz, 2

It need scarcely be pointed out that the presence or absence of concomitant reflex movements as an index of the awakened corpuscular activity of the cord is a most important factor to be borne in mind, but the diminution occurs even when a more pronounced stimulus of greater duration is used, as is shown by the following experiment on a *Rhesus* Monkey. The cord was divided at the 8th dorsal vertebra, and prepared for galvanometric observation. The right sciatic was excited and evoked a reflex movement and large effects, indicated in repeated observations by deflections of 210, 300, and 308. The left sciatic gave effects of 230, 250. After section of both posterior columns, the effect sank to 55 and 58 following excitation of the right nerve, and to 90 and 60 following excitation of the left nerve.

If now we sum up the various readings (15) obtained in two Cats and two Monkeys, we find, as expressed in the following table, that the intervening section reduces the massed results in the ratio of 100 to 22, that is, both the posterior columns are directly concerned with the production of 78 per cent of the total effect, and the transmission of the same percentage of impulses.

TABLE of Readings Section of Posterior Columns

	Cord investigated at	Deflection before section	Deflection after section
Cat	10th dorsal vertebra	75	12
"	"	64	12
"	10th to 11th dorsal	210	39
Monkey	7th dorsal (average of six readings)	96	18
"	8th dorsal	210	55
"	"	300	58
"	"	308	57
"	"	230	90
"	"	250	60
		1743	389
Ratio 100 to 22			

This relationship is confirmed by a control experiment of the reverse kind in which a

section of the part of the cord ventral to the posterior columns was made. The cord was prepared in a Cat by division at the 8th dorsal vertebra, the upper end of the lower fragment connected with the galvanometer, and the left sciatic stimulated with three different strengths of stimulus, and the effect noted in each case. An intervening section was then made at the 10th dorsal, so as to divide the whole region of the cord lying ventrally to the posterior commissure and the commissure itself, the result being that the minimal effect remained unaltered whereas the other effects were diminished in the ratio of 100 to 76, as indicated in the subjoined table

Strength of stimulus	Effect before section	Effect after section
500	35	35
1000	70	56
2000	90	65
Ratio 100 to 76		

This experiment, whilst it establishes the importance of the posterior columns by furnishing the control experiment of leaving these tracts and excluding the others, is at the same time a remarkable instance of the quantitative precision of the method, since in independent experiments lesions effected quite differently show in the one case that the posterior columns are concerned with 78 per cent, in the other with 76 per cent of the effect. As the experimental details accumulate, this steady quantitative relation will be found to vary wonderfully little, considering the nature of the structure investigated and the difficulties connected with the method.

The experiment just alluded to also indicates a very important fact which will be referred to in detail in the concluding section of this work, namely, that when the stimulus is minimal the nerve impulses are almost entirely confined to the direct path, in other words, this path is that of least resistance. It is necessary for the stimulus to be of a certain intensity before nerve impulses can be started of sufficient volume to break through corpuscular structures and so enter on indirect paths. This is indicated by the fact that no change in the deflection could be observed in the case of the weak initial stimulus to follow the section of the grey matter, presumably, therefore, the cord effect was due, in this case, to afferent impulses passing up the direct path.

A further extension of the experiment just described may be now referred to, namely, the influence of dividing in addition one posterior column. After the section of the anterior or ventral portion of the cord the left posterior column was divided at the 10th dorsal vertebra; on now stimulating the left sciatic nerve an effect of 8 only was obtained, this observation being repeated several times. The importance of the posterior column on the side of the nerve is thus forcibly brought into view,

*B. Section of the Posterior Column of the same side as the Nerve Excited.*

The marked diminution in the effect obtained by hemisection on the same side as the nerve in the one case, and by section of both posterior columns in the other, would seem to imply that the posterior column on the same side, which is common to both these lesions, is the fundamental structure concerned. We shall see that there is every reason to suppose that it is concerned with 60 per cent. of the total effect, that is, with that proportion of the number of nerve impulses, the remainder being pretty equally divided between the lateral column of the same side and the posterior of the opposite side. It will be seen that the direct evidence of the result of section of one posterior column is somewhat complicated by changes in excitability which appear to affect the remaining columns.

The results were observed in two Monkeys and five Cats, as shown in the following Tables —

SECTION of Posterior Column on Same Side as Nerve.

	Cord observed at	Before section	Section at	After section
		Deflection		Deflection
Monkey ( <i>Macacus</i> <i>rhesus</i> )	8th dorsal vertebra	130 210 304	10th dorsal vertebra	38 68 100
Monkey ( <i>Macacus</i> <i>rhesus</i> )	A dorsal vertebra (the 8th probably)	32 60 78	11th dorsal vertebra	12 21 14
		814		252
Ratio of 100 to 31				

In these Monkeys section of the posterior column on the same side reduced the cord effect by 69 per cent., a very notable amount. Such a large reduction was not often obtained in the Cat, and occasionally in this animal comparatively insignificant reductions were seen. In such instances, however, the nerve stimulation was observed to evoke violent reflex movements, and, as will be seen in considering the result of section of the opposite posterior column, the opposite uninjured side of the cord became evidently hyperexcitable.

SECTION of posterior column on same side as nerve at 11th to 12th dorsal vertebra.

Cord observed at 8th dorsal	Deflection before section	Deflection after section
I Cat	90	35
II Cat	100	38
	75	34
III Cat	76	45
	83	24
IV Cat	210	115
V Cat	185	96
	185	121
	1004	508
Ratio of 100 to 50		

The above experiments made upon five Cats give results, which, as is seen, differ considerably in several instances, the deflection before section being in some cases four times as great as that after section, in others not twice as large. The latter is, however, the case when owing to some circumstance the stimulus evoked very large effects (see Cats IV. and V) including strong reflex movements. If, however, we mass together all the results obtained in the two sets of animals, the average reduction of effects due to section of one posterior column would amount to about 60 per cent of the total effect obtained in the normal condition. Hence it would seem that one posterior column is the main channel by which the entering nervous impulses proceed from the lumbar to the dorsal cord.

The difficulties involved in this series of experiments will be still more evident when we turn to the influence of the section of only the opposite posterior column upon the cord effect.

### *C. Section of the Posterior Column of the Opposite Side to the Nerve Excited*

In these experiments we are for the first time confronted with the remarkable fact that in consequence of an intervening section the stimulation of the nerve is sometimes followed by an increased effect. (See also Chapter VIII, Section 9, B., p 395) Since the section has cut off at least some channels of communication between the lower and upper parts of the cord, and presumably, therefore, has blocked the paths of some, even though few, nerve impulses, such a rise must be attributed to the greater intensity of the effect evoked in the remaining channels, whether nerve fibres or nerve cells, and the cord must therefore be considered to be hyperexcitable.

This alteration in excitability is probably associated with the phenomenon of hyperaesthesia observed by FODERA and SCHIFF to follow operative interference with the



posterior columns. That it affects the cord on the side of the lesion is probable from the results just given, but the direct proof is wanting since the increased intensity of the effect is masked by the large diminution caused by the severance of the direct tract in the posterior column of the same side. There is, however, no such severance in the case of the opposite side, and the increased excitability is plainly seen, as evidenced by the cases marked with an asterisk, in which the section was followed by actual increase in the cord effect. Whatever may be the meaning of this it undoubtedly is a most important factor to be taken into consideration in all experiments the general plan of which consists in first causing definite lesions, and then examining the influence of such. It will be obvious too, that in proportion as the anæsthetic is removed so much the more marked must this change in excitability become. In the experiment upon conduction already referred to, made by MIESCHER, in which the reflex effect on the blood pressure was taken as the index of the passage of afferent impulses through a block in the cord, any change of this kind could not be allowed for as owing to the curarisation of the animal, the observation of concomitant reflex movements was impossible. We venture to think that the increased effect obtained by MIESCHER on the side of the complete section in his division of every part of the cord except one lateral column, and taken by him to mean that the afferent fibres crossed into the lateral of the opposite side, was due to some such increased excitability in the lower fragment of cord on the side of the main lesion, the fibres of the lateral tract connecting this fragment with that above as internuncial fibres.

It is obviously impossible to put this factor completely out of court. The cord effect with which we are dealing is a measure at once of the intensity and the number of all transmitted excitatory processes, and the influence of any particular section can therefore only be judged of by taking the average of all the readings, high and low. It might be thought that by pushing the anæsthesia and by decreasing the strength of the stimulus the effect would always become uncomplicated. Although anæsthesia lessens the chance of its occurrence it would appear that this increase in the cord effect will sometimes occur even under these conditions, and it is then evidently dependent upon the character of the particular preparation used. Its presence or absence in these cases may, however, be not merely due to the idiosyncrasy of the animal, but to minute differences in the extent of the lesion in certain instances.

The general result of experiments on four Cats and two Monkeys is as follows —

EFFECT of Section of Posterior Column at the 10th to the 12th Dorsal Vertebra on the Opposite Side to the Nerve Excited.

	Cord observed at	Nerve excited before section		Nerve excited after section	
Cat (196)	10th dorsal	105 128 107	111	52	
Cat (250)	8th dorsal		78	87*	
Cat (377)	9th dorsal		78 125	90* 91	
Cat (349)	9th dorsal		182	121 180	150
Total			574		470
Ratio 100 to 81					

	Cord observed at	Nerve excited before section		Nerve excited after section	
Monkey (281)	8th dorsal	155 230 250		150 170 199	
Monkey	7th dorsal	65 82 96		105* 87* 120*	
Total .			878		831
Ratio 100 to 94					

From these results it is seen that the cord effect is reduced by the section, and that this reduction in the observed cases was more marked in the Cat than in the Monkey. If we take the two sets of experiments together, as in the previous results of the division of the posterior column of the same side, then the reduction is found to be from 100 to 87, that is, 13 per cent.

This evidence therefore points to a crossing of effects from one side of the cord to the other as probable, such crossing and the ultimate conveyance of the impulses being more or less bound up with the posterior column on the opposite side to the stimulated nerve, to the extent of 13 per cent. in the animals we have as yet examined.

*D. Previous Section of Posterior Columns some time Previous to Observation*

In one Cat (251) we divided the posterior columns at the level of the 10th dorsal vertebra four weeks before the experiments. When the animal (Cat) was examined it was noticed that the water test showed diminished sensibility in both hind feet, since the animal could be placed with its hind paws in water without exhibiting any movements of withdrawal. There were, however, vague symptoms that the two sides were not equal in the degree of sensibility they still possessed. This inequality showed itself in the knee jerks, the left being much feebler than the right. On placing the animal under ether, however, the left knee jerk was found to be then very much exaggerated, and the left hind limb was easily sent into a condition of clonic spasm.

The animal was first experimented upon by exposing and exciting the cord, and observing the changes in the nerves, the result of this experiment will be given in Chapter X. It was then used for the present series of experiments, the cord being originally divided at the 5th dorsal vertebra, and the upper end of the lower fragment prepared for galvanometric observation at about the 7th dorsal vertebra.

The left sciatic, when excited, with a minimal and a stronger stimulation, evoked effects of 10 and 20, the right, when similarly excited, evoked cord effects of 8 and 70.

The cord, after the death of the animal, was examined histologically, when it was found that the section had not been complete on the right side, a good many fibres having been left intact. On the left side it was complete, and at the level of the 7th dorsal, on microscopical examination, a sickle-shaped patch of degeneration could be seen in the postero-external column on each side, that on the left being very well marked, whilst that on the right was small. The same difference between the degeneration on the two sides could be seen at the level of the 4th cervical, where the degenerated area occupied, on the left side, a conspicuous portion in the middle third of the posterior median column. The discrepancy between the effects obtained between the two nerves is thus cleared up by the minute examination of the extent of the lesion. It furnishes striking evidence of the accuracy with which the electrical method can gauge the integrity of through tracts of fibres, but brings out a disadvantage, namely, that it involves the death of the animal, hence, when lesions, &c., are made *at the time* of the experiment, it is impossible to be perfectly certain of their extent, since the degeneration method, which alone would give absolute indications, cannot then be used.

**SECTION 8.—INFLUENCE OF SECTION OF THE LATERAL COLUMN.**

Of the remaining columns in the cord, the lateral and anterior, it is only the former which appear to bear any relation to the production of the electrical effect in the

cord when the sciatic nerve is excited. This is shown by the fact that the cord effect is in no way modified by an interruption in the anterior columns which involves their complete severance, caused by a section between the entering nerve and the observed region. Such a section is most easily made in the isolated fragment of cord near its central attachment, since this portion is raised from its bed. This is in strict accordance with the fact alluded to in Chapter VIII, that excitation of the one end of the anterior column evokes no electrical effects in a distant portion of the cord.

It is otherwise with the lateral columns which have distinct relations with electrical effects in the cord, since, as shown in Chapter VIII., their stimulation evokes marked cord effects. It does not follow, however, that this relation is one which comprises the afferent nerves, for we know that the lateral column contains the main path for the efferent cord tracts, as is shown by the results of cortical excitation, as set forth in Chapter V, &c. The conclusion at which so many observers have arrived, that the main afferent path, whether crossed or uncrossed, is situated in the lateral column, is clearly not substantiated by any evidence offered by the employment of the present method, since the integrity of the two posterior columns is evidently essential for the production of at least 70 per cent of the total effect. We shall see that the extent to which the two lateral columns are related to the afferent effect is small, being approximately only a fourth part of this amount, and that this is almost entirely confined to the lateral column on the same side as the afferent nerves excited. The results may be best displayed as follows.—

*A. Effect of Section of the Lateral Column on the same side as the Nerve Excited*

The following experiments made upon four Cats show that the lateral column of the same side as the excited nerve, if divided, reduces the cord electrical effect evoked by excitation of the nerve to an extent the average of which is 20 per cent, that is, from 100 to 80.

## SECTION of Lateral Column on the same Side as the Nerve Stimulated.

	Cord observed in region of	Effect before section	Section at	Effect after section
Cat (196)	10th dorsal vertebra	105	1st lumbar	115*
Cat (327)	9th   "       "	105	1st lumbar	76
		132		83
Cat (346)	8th   "       "	90	1st lumbar	60
		110		105
		542		439
Ratio 100 to 80				

The inference is that the integrity of the lateral column of the same side is connected with 20 per cent. of the cord effect. Additional ground for this conclusion is afforded by the opposite sectional method practised after the manner of MIESCHER and WOROSHILOFF, which, excluding the lateral column, divides everything else; the knife being placed perpendicularly through the cord from dorsal to ventral surface at the junction of the posterior and lateral columns, and then the cut made obliquely inwards towards the centre, and continued so as to come out on the opposite side. All the structures, with the exception of one lateral column, and the contiguous portion of the lateral horn are thereby severed. In some instances this operation was done piecemeal, first one and then another structure being divided.

The result of such severance of both posterior and one lateral column is to show that an electrical effect in the cord can still be obtained by stimulating the nerve on the same side as the uninjured lateral column. Its amount, as compared with the total change obtained before the section, is, however, greatly reduced, as is shown in the following Table, comprising experiments made on five Cats.

\* It will be noted that in Cat 196 there ensued an increased effect after the section due to a rise in excitability.

## SECTION of both Posterior Columns and Lateral on opposite Side to Nerve.

		Effect before section.	Intensity of stimulus	Effect after section
(195) Cat	. . . . .	210	4000	6
(196) Cat	. . . . .	86	4000	8
(256) Cat	. . . . .	78	1000	23
(327) Cat	9th dorsal vertebra	142	1000	35
(344) Cat	8th     "     "	6	500	28
		122	1000	35
		152	2000	27
		856		162
Ratio 100 to 19				

That is to say, this remaining effect represents 19/100 of the whole. This result tallies with that obtained with the other method, which showed that the section of this lateral only reduced the effect by about 20 per cent. This reduction in the cord electrical change is thus a reduction in the number or intensity of the afferent impulses which pass up the cord when the nerve is excited. Hence, as far as the method goes, it would appear that the lateral column on the side of the stimulated nerve furnishes a path, whether internuncial or not, we cannot say, but, at any rate, an indirect one for the transmission of 20 per cent. of the nerve impulses.

B *Effect of Section of the Lateral Column on the opposite side to the Nerve Excited.*

The contradiction which exists between the results of the present research and the interpretation given to their experiments by MIESCHER and WOROSCHILOFF is brought into the strongest prominence by the consideration of the present group of results. If the interpretation of these physiologists is warranted by their data, and is of general application, then we should expect that the integrity or otherwise of the lateral column opposite the entry of a stimulated nerve would have the preponderating influence upon the passage of those nerve impulses which have entered the cord by the nerve, and consequently upon the amount of the electrical change in the observed portion of cord. We have, however, already accounted for 95 per cent. of the effect by showing that the amount is dependent upon the integrity of the other columns, and this fact alone is sufficient to show what a small share the integrity of the opposite lateral column has in providing channels for the conduction of ascending impulses.

We have made experiments upon five different animals, the results being separated into those in which the lateral column was divided on the opposite side to the nerve, and those in which all structures, except the opposite lateral column, were cut out.

INFLUENCE of Section of the Lateral Column on the opposite Side to the Excited  
Nerve on the Cord Effect.

	Cord divided and observed at	Effect before section	Stimulus	Effect after section
(196) Cat	10th dorsal vertebra	86	4000	100
(327) Cat	9th   "   "	82	500	78
		142	1000	125
(346) Cat	9th   "   "	110	1000	63
		110	2000	112
		530		478
Ratio 100 to 90				

It will be noticed that in only one case (346) was there any marked reduction, and that this did not occur when the intensity of the stimulus was increased. Instead of reducing the effect the section in two cases increased it. The average reduction of 10 per cent. is probably too high, owing to some unknown factor being present to cause the exceptional low reading. This presumption is rendered more probable by the next set of results, the converse experiments

SECTION of all Columns except Lateral on Opposite Side to Excited Nerve.

	Cord divided and observed at	Effect before section	Stimulus	Effect after section
(196) Cat	10th dorsal vertebra	105	4000	10
(256) Cat	8th   "   "	90	1000	0
(327) Cat	9th   "   "	142	1000	5
		105	500	5
(344) Cat	8th   "   "	74	500	3
		93	1000	15
		135	2000	3
		734		41
Ratio 100 to 6				

These results show that at any rate under the conditions which were present in these experiments, those, namely, of moderate narcosis, the lateral column of the cord opposite to the nerve excited can transmit only 6 per cent of the nerve impulses which produce the electrical change in the cord when all the other structures are divided. To what extent it can act as a bridge when the ether is removed, as in MIESCHER



and WOROSCHILOFF'S experiment we have not yet had an opportunity of observing. The experiments would have to be done under curare to avoid the dragging on the cord by the convulsive movements of the animal and without anæsthesia, analgesia being provided for by section of the peduncles. They are, therefore, of a very special kind, and involve much consideration before embarking upon them.

#### SECTION 9.—SUMMARY

We will now sum up the results of the foregoing experiments, pointing out at the same time the deficiencies as well as the advantages of the method employed

I. Electrical changes in the lower dorsal region of the cord are readily evoked by excitation of the sciatic nerve, or the posterior roots of the lumbar plexus.

II. These changes are dependent in the anæsthetised animal on the integrity of particular columns of nerve fibres stretching between the region observed and the neighbourhood of the entering nerves.

III. The total amount of electrical change is an indication of the amount of nerve energy flowing up the cord from the stimulated nerve. If the total amount be represented as 100, then the following numbers represent approximately the amount which flows up each column and which is thus interrupted by its section.—

Posterior column same side . . . . .	60
Posterior column opposite side . . . . .	15
Lateral column same side . . . . .	20
Lateral column opposite side . . . . .	5

IV. The flow of nerve energy up the cord is thus mainly unilateral, 80 per cent. being transmitted in the channels on the same side as the entering nerve.

V. The comparatively small amount of nerve energy which crosses into the opposite side of the cord is almost entirely localised in the posterior column of that side

These conclusions are, it will be observed, simply confirmatory of those already indicated in the preceding chapter, in which it was pointed out that no electrical evidence existed of any crossing of ascending impulses in the cord from the fibres in one lateral column to those of other columns; and that the peculiarity of the ascending impulses in the cord is (a) the direct path they take up the posterior column of the same side, and (b) the indirect path by spread from the posterior column, first into the lateral column of its own side, and then across into the posterior column of the opposite side.

Finally, our experiments do not show the path taken by sensory impulses; it is possible, though hardly conceivable, that these are essentially different in quality to the ones we have been studying. All we can say is that when nerve impulses are evoked in the afferent fibres of the sciatic nerve, and proceeding up these reach the cord, they apparently find several paths open to them. These paths, however,

are either not equally numerous, or are not equally easy of passage, the posterior column of the same side offers special facilities for the passage of the impulses, the lateral column of the same side offers facilities greater than the posterior column of the opposite side, but both, whilst far inferior in this respect to the posterior column of the same side, are far superior to the remaining lateral column of the opposite side. This last, at least in the narcotised animal, offers practically no facilities for such passage

It is, perhaps, unnecessary to draw attention to the circumstance that the above results are only verified in the case of the lower dorsal region of the cord in the Cat, and to some extent in the Monkey.

The principal deficiencies of the present method have been indicated in this and previous chapters, but may now be summarised. They are connected—

(a) With the character of the nerve impulses, which, being due to electrical excitation, are more intense, and possibly different in quality, to those which are generated in peripheral sensory end organs

(b.) With the necessity of insulating the observed portion of cord, to ensure the observation of localised effects in it, this being accomplished by a severe operation which entails the death of the animal at the close of the experiments

(c.) With the limited anatomical scope of the method as at present used, the highest point which we have reached being the mid-dorsal region. The shock of the exposure above this has rendered our experiments, carried out higher than this, unsuccessful.

The chief merits of the method are—

(a) That the changes investigated are the electrical excitatory processes in the cord itself severed from the encephalon, and are free, therefore, from admixture with cerebral effects, and are independent of the reflected outcome of such effects in the muscles.

(b.) That the changes are so definite as to admit of comparison as to their quantity, and thus of a quantitative estimate of the nerve energy transmitted in the cord under different conditions.

(c.) That this quantitative character of the results enables a comparison to be made of the effects of nerve energy which are dependent respectively on the integrity of the different parts of the cord.

The conclusions to which we have thus arrived will receive additional confirmation from the results of experiments in which the impulses in the nerves are made the subject of investigation by the electrical method, such impulses being aroused by excitation of the different columns in the cord.

These will be detailed in the next chapter, at the end of which a general review of the whole question of conduction in the cord, as elucidated by our method, will be given.

## CHAPTER X—ELECTRICAL CHANGES IN THE NERVES FOLLOWING EXCITATION OF THE SPINAL CORD

Section 1 —Introductory.

Section 2 —Plan of experiments and preliminary observations

Section 3.—Electrical effects in sciatic nerve following excitation of different columns of the cord

Section 4 —Electrical effects in afferent nerves following excitation of the cord

(1 ) Posterior roots.

(2 ) Sciatic nerve after section of anterior roots

Section 5 —Electrical effects in efferent nerves following excitation of the cord

Section 6.—Influence upon the effects in the nerve of intervening sections of the cord

A Influence of hemisection.

B Influence of section of the posterior column on the same side.

C Influence of section of the posterior column on the opposite side

D Influence of section of both columns

E Influence of section of the lateral columns.

Section 7 —Summary and conclusions.

### SECTION 1.—INTRODUCTORY.

In the foregoing chapter the results have been given of the observation of a new index of cord activity, that of noting the accompanying electrical effects when the afferent nerves were excited together with the influence upon these of a series of intervening sections.

It will be seen that the plan of the whole of that research was upon the lines of previous investigations, except as regards the index employed, in the experiments to be detailed in this section both the method and plan of experiment are entirely novel, since conclusions can only be arrived at by the evidence afforded by the electrical effects as indicative of the presence or absence of excitatory changes. The novelty consists in this, that we are able to detect excitatory electrical effects in the issuing nerves when the cord is stimulated; not merely in the nerves themselves, but in their roots. Now as far as the efferent motor roots and motor portion of the mixed nerves are concerned, the method whilst giving us valuable information has obvious relations with the data which have already been obtained by the graphic method of recording the muscular contractions, but as far as the afferent sensory nerves are concerned, it introduces us to previously unknown relationships, for there is no indication other than an electrical one at present known, which can detect the passage of nerve impulses from the cord into afferent tracts, since such passage is opposed in direction to that of the normal transmission as usually understood. It has been already stated that one of the most valuable results of the discovery of the excitatory electrical change was that set forth by DU BOIS-REYMOND, as proving the propagation of excitatory effects in both directions along a continuous tract of either afferent or efferent nerve fibres, this being evidenced by the presence of the electrical change at

both ends of a nerve when the middle portion is stimulated. We have seen that similar evidence in the case of the nerve fibres in the cord shows that in them also the effect is propagated from the stimulated region indifferently either towards the centre or the periphery, and it follows from the combination of these two, that if any fibres in a nerve are directly continuous with those in the cord, the excitatory changes following stimulation of these must be propagated along the whole length of the continuous strand and may thus travel out into the fibres of the nerve. Direct continuity has been shown to exist by the degeneration method between the fibres of the posterior root and those of certain portions of the posterior columns, hence it is not surprising that the stimulation of the posterior columns in the cord should cause electrical changes in the posterior root due to the arrival in the fibres of this structure of excitatory processes transmitted from the cord down tracts which, owing to their terminal relations, are usually believed to be solely ascending ones. There is nothing to warrant the belief that these descending impulses in afferent nerves, evoked by excitation of the columns in the spinal cord, are in themselves different from those which are evoked by similar methods of excitation when applied to the peripheral parts of the afferent nerves, and which are propagated in the natural direction, since it seems to be fundamental as regards nerve conduction that fibres can conduct equally in either direction.

The fact that in one group of nerve fibres (afferent) the starting platforms are at the peripheral end, and the receiving termini at the central, whilst in the other (efferent) the positions are reversed, and that, in consequence, what are called normal nerve impulses proceed in the afferent direction in the one group and in the efferent in the other, apparently has not, physiologically or structurally, altered the fibres (polarised them in any way) so as to make conduction in the one direction more difficult than in the other. As far, then, as the directly continuous afferent fibres are concerned, there is no difficulty either in obtaining electrical results in the posterior roots on exciting their direct prolongations in the cord, or in interpreting these as indicative of the passage of nerve impulses.

A much more complicated condition must, however, be now referred to, that, namely, of the nerve fibres which are only indirectly continuous with others in the cord, there being interposed in their path corpuscular elements and unknown channels.

The simplest of these are the efferent (motor) nerves, and it has already been stated that, as regards these, Chapter IX., Section 2, the corpuscular connection is of such a character that, whilst allowing the passage of impulses from the cord to the nerves, it appears to completely block the passage of impulses from the nerves into the cord. (See also Chapter XI., Section 2 (1).) The stimulation of a mixed nerve (the posterior roots being divided) or an anterior root thus evokes impulses which travel up and break upon the shore of the nerve corpuscles, and either remain on

their peripheral side, or issue in such broken and disorderly array that their character is completely lost, and all evidence of their presence disappears.

To what extent is this true of the afferent root fibres? The answer to this question is one which can only be appreciated when the results of the experiments of both this chapter and the succeeding one, upon the reflex functions of the cord, have been analysed; but it may be well here to state at once that there is no evidence of such pronounced block to impulses which may be caused to descend the indirect paths by which the posterior root fibres are brought into connection with the cord.

The difficulties of interpreting the experimental results are increased by the gap which exists in our anatomical knowledge as to the connection between these indirect afferent fibres and the cord. This connection is one upon which the degeneration method throws but little light, although it would appear probable from the trophic changes observed, and from morphological considerations, that there are cells in the posterior horn, and possibly in CLARKE'S column, which are connected with fibres in the posterior roots (MOTT). The recent researches of KOLLIKER seem to indicate that the termination of some of these indirect fibres in the cord is largely that of a fine plexus with free ends.

Although the central connections of the fibres are as yet to a great extent unknown, yet the description indirect as distinguished from direct is warranted by its wide-spread use. It is advisable, however, to emphasise what the term indirect as used by us in the present case is understood to connote.

It is descriptive of all afferent fibres in the cord, which may be supposed to be connected with those of the posterior root, but which do not show any of the degenerative and developmental differences which stamp some fibres (posterior median) as being in direct continuity with the root. There is, however, nothing in itself to show that this term indirect is a strictly logical one; since the same line of argument might be applied to those fibres which pass through the ganglion on the posterior root, with regard to which the degeneration method furnishes no evidence of direct continuity (JOSEPH).

Impulses are conducted through the ganglion in either direction (DU BOIS-REYMOND), and apparently without any modification in their time relations (EXNER) if we may suppose that this is due to the fact that, apart from the few fibres which appear not to come into relation with cells at all, the relationship of the majority of fibres to the ganglion cells is of the T-piece kind, as shown by RANVIER, in which case the cell does not interrupt the continuity of the connected fibre. There is no reason why some such sort of bypath (GOLGI) may not be the basis of the connection of the fibres with the corpuscular elements in the spinal cord, as it is in certain parts of the cerebrum (FLECHSIG).

There are, therefore, no anatomical data which are necessarily implied in the term indirect as applied to these fibres, beyond the fact that such fibres come into

connection in some way with some element in the cord, which serves as a common centre both for nutrition and for growth

The researches on the conduction of afferent impulses from the nerves into the cord detailed in the preceding chapter, as well as our other experimental investigations, show that such paths undoubtedly exist. The present experiments will prove that these, although indirect, are capable of conducting impulses from the centre towards the periphery; the only distinction between the indirect and the direct path, in this respect, being the greater intensity of the stimulus necessary to produce the evidence of such effects in the case of the former, and the comparatively small amount of the nerve energy which can be thus evoked through the indirect path, in the afferent nerves. In other words, the direct path is that of least resistance to impulses when these pass backwards from the cord into the afferent nerves.

We now pass to the consideration of the detailed plan of the experiments as a necessary prelude to the analysis of the results.

## SECTION 2 — PLAN OF EXPERIMENTS AND PRELIMINARY OBSERVATIONS

Our first experiments upon the nerve effects following cord excitation were crude in design. They were made by first dividing the cord in the dorsal region, then preparing one sciatic nerve in the back of the thigh, ligaturing it, dividing it, and connecting its central end and the adjoining longitudinal surface by means of cable electrodes with the galvanometer, and finally stimulating the cord by means of needles which pierced it and acted as electrodes to the secondary coil of the inductorium. We satisfied ourselves in this way that the excitation of the cord was followed by excitatory electrical changes in the nerve, and then proceeded to more methodical experiments. In these the cord was carefully exposed by dissection and a piece removed, so that the cross section of its surface could be easily seen. The various cut ends of the columns were then excited as desired by a series of interrupted induction currents (Helmholtz side-wire) for a period which was controlled by the revolving mercurial key, and was carefully kept of the same duration during any set of observations. A pair of well-insulated fine platinum-pointed electrodes were used for the stimulating current, these being applied to the particular region of the cross section it was desired to excite, in the manner and under all the precautions already described in Chapters III and VIII. The sciatic nerve when raised in air and connected with the galvanometer displayed the usual resting electromotive difference between its two points of contact. This difference has been referred to at length in Chapter IV and was compensated in all cases. On exciting the cord for five seconds an electrical effect was produced in the nerve which was always opposed in direction to the resting current, and which passed away on the cessation of the stimulus. The amount of the deflection was in most cases considerably less than was obtained by applying the same stimulus (unaltered in intensity and duration)



to the trunk of the nerve. It was notably affected by several conditions, of which the most important are those affecting the state of the animal and those connected with the intensity of the stimulus. The influence of these two conditions demands closer examination.

The state of the animal has the greatest influence on the amount of the change. To take the most powerful factor first, the systemic death of the animal, this is at once shown in the diminishing size of the effect, until, in about ten minutes, no electrical change can be evoked in the nerve when the cord is excited.

The following experiment may be quoted in illustration of this point, it is one in which the posterior root instead of the nerve was observed.

The cord of a Cat was divided at the 10th dorsal and the cauda equina exposed. The 7th lumbar posterior root on the left side was then ligatured and divided near the ganglion, raised in air and its central end and surface connected with the galvanometric electrodes.

Excitation for five seconds of a given tract in the cord (the left posterior column) evoked an electrical change indicated by a galvanometric effect of 253. The animal suddenly died from collapse, the heart failing, and the experiment was then repeated about four minutes after death, when the deflection was found to be less, viz, 165.

The time of this observation was 12.1. A series of such observations were then made as follows —

Time	Deflection
12.1	165
12.2	142
12.3	139
12.5	75
12.7	50
12.10	8
12.12	nil

Excitation of the root itself still evoked considerable effects at 12.15. We have often had the opportunity of noting that the nerve electrical effect when evoked by excitation of the cord, disappears on death earlier than when evoked by excitation of the nerve trunk. This we imagine to be due partly to the circumstance already mentioned that the latter excitation produces normally a more marked effect than the former, and partly to the changes in excitability which, in accordance with the Ritter-Valli law, proceed from the centre towards the peripheral attachment of a nerve.

A more important influence than this of death, since it is one present throughout all the experiments, is that dependent upon the varying degree of anæsthesia. There are many experiments which furnish illustrations of this point. A stimulus of the same character, intensity, and duration, applied to the same region of the cord, evokes



now a larger and now a smaller effect, dependent upon marked lessening and deepening of the narcosis. The importance of bearing this in mind is sufficiently obvious, it is, however, capable of control, since the character of the movements awakened by the stimulus furnishes a fair index of the condition of anæsthesia, and was in all cases closely observed.

Finally, the influence of temperature is one to which attention has already been directed in Chapter III, and although the necessity of keeping the exposed cord covered with warm sponges, except during the actual stimulation, has been already dwelt upon, it may be insisted on again at this juncture.

Alterations in the duration and intensity of the stimulus modify the effect; the longer the duration and the greater the intensity, the more pronounced is the nerve change. The modifications are so marked, that in analysing and comparing the quantitative value of the nerve effects obtained by stimulation of different regions of the cord, it will be necessary to divide the indicative galvanometric deflections into two classes, as evoked by "minimal" and maximal stimuli respectively. It will be understood, however, that a rigid separation is impossible, there being every grade between an undoubtedly "minimal" effect with no accompanying reflex movements and an undoubtedly maximal effect with vigorous movements.

The experiments were made upon twenty-one Cats and six Monkeys, and may be divided into four groups, the first three of which differ as regards the nerve fibres in which the electrical change was observed, the fourth differing as regards the condition of the cord, through the stimulation of which the nerve effect is evoked. We have, therefore, to consider in succession.—

The electrical effect in the mixed sciatic nerve;

„ „ „ afferent nerve roots;

„ „ „ efferent nerve roots;

The modifications produced by intervening section of tracts in the cord.

Each group will form the subject of a succeeding section.

### SECTION 3—THE ELECTRICAL EFFECTS IN THE SCIATIC NERVE FOLLOWING EXCITATION OF THE DIFFERENT COLUMNS OF THE CORD

The experiments upon this subject will be best displayed by first selecting and describing the results of a particular experiment in the Cat and Monkey respectively, and then giving a table which will show the averages of all the comparable observations.

The spinal cord was exposed and divided in an anæsthetised Cat (331), at a level between the 10th and 11th dorsal vertebræ; both the sciatic nerves were then carefully exposed, ligatured in the lower part of the thigh, and divided on the peripheral side of the ligature. They were then freed from their attachments and raised in the

air by the ligature. A separate pair of non-polarisable electrodes was placed in connection with the cross section and the surface respectively of each nerve. A piece of cord 1 centim long was now removed from the upper end of the lower fragment of the cord, thus exposing a fresh cross section of all the columns.

The left sciatic nerve showed a resting electrical difference between the surface and cross section, which was balanced by a difference of 01 Daniell, the right nerve showed a rather less marked difference balanced by 008 Daniell.

Each pair of nerve contacts was alternately connected with the galvanometer, a Pohl's reverser without cross wires being used to switch either set of contacts into connection. The following deflections, opposed in direction to the resting difference, were obtained from the nerve when the cut ends of the various columns designated below were excited for 5 seconds —

#### LEFT Nerve connected

Strength of stimulus	Region excited	Effect
Secondary coil 500	Left posterior column	140
	Left lateral        ,,	Nil
	Right posterior   ,,	15
	Right lateral     ,,	Nil
	Anterior columns	Nil

#### RIGHT Nerve connected

Strength of stimulus	Region excited.	Effect
Secondary coil 500	Left posterior column	5
	Left lateral        ,,	Nil
	Right posterior   ,,	65
	Right lateral     ,,	Nil
	Anterior columns	Nil

The intensity of the stimulus was now doubled.

#### LEFT Nerve connected

Strength of stimulus	Region excited	Effect
Secondary coil 1000	Left posterior column	190
	Left lateral        ,,	5
	Right posterior   ,,	30
	Right lateral     ,,	Nil

## RIGHT Nerve connected

Strength of stimulus	Region excited	Effect
Secondary coil 1000	Left posterior column	5
	Left lateral     "	Nil
	Right posterior   "	132
	Right lateral     "	Nil
	Anterior columns	Nil

Intensity of stimulus again doubled

## LEFT Nerve connected.

Strength of stimulus	Region excited	Effect
Secondary coil 2000	Left posterior column	240
	Left lateral     "	16
	Right posterior   "	40
	Right lateral     "	Nil
	Anterior columns	Nil

## RIGHT Nerve connected

Strength of stimulus	Region excited	Effect
Secondary coil 2000	Left posterior column	15
	Left lateral     "	Nil
	Right posterior   "	172
	Right lateral     "	5
	Anterior columns	Nil

The above experiment shows plainly that, with a weak stimulus, an effect is only produced in the nerve by stimulating the posterior columns, and that this effect is very marked when the directly continuous fibres in the posterior column of the same side as the observed nerve are excited, and is small when the fibres of the posterior column of the opposite side are excited. A very small effect is produced by stimulating the lateral columns until the stimulus is strong, and even then an appreciable effect is obtained only from the excitation of the lateral on the same side as the nerve.

A similar experiment may now be quoted in detail upon the Monkey (333) (*Macacus sinicus*). The cord was divided in the anæsthetised animal at the 10th dorsal vertebra, so that the cut ends of the various columns could be excited as in

the previous experiment. Both nerves were then prepared and connected alternately with the galvanometer in the manner already described. The excitatory electrical effects in each nerve following the stimulation of the different columns of the cord were observed with different intensities of stimulus, and the results, which are analogous to those obtained in the Cat, are shown in the following Table. The left nerve was found to be less excitable than the right, but the resting difference of both was 0.05 D.

## LEFT Nerve connected

Intensity of stimulus	Region of cord excited at cross section	Deflection of galvanometer
2000	Left posterior column	14
	Left lateral       ,,	Nil
	Right posterior   ,,	3
	Right lateral     ,	Nil

## RIGHT Nerve connected

Intensity of stimulus	Region of cord excited at cross section	Deflection of galvanometer
2000	Left posterior column	12
	Left lateral       ,,	Nil
	Right posterior   ,,	68
	Right lateral     ,,	10

Intensity of stimulus doubled.

## LEFT Nerve connected.

Intensity of stimulus.	Region of cord excited at cross section.	Deflection of galvanometer
4000	Left posterior column	106
	Left lateral       ,,	25
	Right posterior   ,,	39
	Right lateral     ,,	Nil
	Anterior columns	Nil

## RIGHT Nerve connected.

Intensity of stimulus	Region of cord excited at cross section	Deflection of galvanometer
4000	Left posterior column	52
	Left lateral        "	Trace
	Right posterior   "	112
	Right lateral     "	6
	Anterior columns	Nil

The effect in the mixed nerve of the Monkey is thus shown to be most strongly evoked when the excitation is that of the posterior column on the same side as the observed nerve. This preponderance over those effects which are evoked in a minor degree from stimulation of the lateral of the same side and the posterior of the opposite side is very marked when the stimulus is minimal.

The two experiments thus quoted form two in a series similarly made upon six Cats and five Monkeys, and the average results of all galvanometric deflections obtained in these form the most reliable data from which to draw any conclusions as to the relations between the amount of electrical change in the mixed nerve and the special regions of the cord which were stimulated. We must, however, again discriminate between effects evoked by stimuli of only just sufficient intensity to ensure their presence, which we term *minimal* (i.e., 500 to 1000), and those which more strongly arouse the region excited, *maximal* (i.e., 2000, occasionally 4000); hence, for every column excited, we have the result of a minimal and a maximal stimulus.

Moreover, it is obviously useless to designate which nerve is connected with the galvanometer, if we place together—

A. All effects evoked by excitation of the posterior column which is on the same side as the nerve.

B. All effects due to excitation of the posterior column on the opposite side to the nerve.

C. Those due to stimulation of the lateral column on the same side.

D. Those due to stimulation of the lateral column on the opposite side.

Any alterations in the stimulation as to intensity and duration necessary in different animals do not affect the value of any comparison between the quantitative results of the members of each different group, since the stimulus was always the same during any one set of observations, and each set included stimulation in regular succession of all the different columns indicated. The total result of such observations in the Cat is as follows:—

## CAT.

Animal	Cord divided at	Effect in sciatic nerve following							
		A Excitation of posterior column of same side		B Excitation of posterior column of opposite side		C Excitation of lateral column of same side		D Excitation of lateral column of opposite side	
		Min	Max	Min	Max	Min	Max	Min	Max
Cat (254)	8th dorsal		85		20				0
			80		8				0
			82		18		12		0
Cat (265)	11th dorsal	36	86	0	32	0	7	0	0
				0		0		0	
Cat (311)	8th dorsal	49	130		20				
			152		26				
			108		36				0
Cat (329)	9th dorsal	50	85	5	25	0	10	0	0
		28	89	5	22		9		
Cat (363)	9th dorsal	42	122	8	10	0	15	0	
		65	145	5	28	0	10	0	
			138		28				
Cat (331)	10th dorsal	65	140	5	15	0		0	
			190		30		5		0
			132		5				
			172		15		5		0
			240		40		16		0
Aggregate sum		335	2178	28	378	0	89	0	0
Average		48	128	6	22	0	10	0	0

From this it will be seen that with the minimal stimulus effects were obtained only on exciting the posterior columns, that the effect, due to excitation of the posterior column on the same side as the nerve, was eight times as large as that due to excitation of the posterior column on the opposite side, and that no effect was produced by stimulation of either lateral column. With a stronger stimulus, it is seen that the effect evoked from the posterior column of the same side was five times as large as that obtained from the posterior of the opposite side, and further an effect was obtained from the excitation of the lateral column on the same side as the nerve.

Turning now to the Monkey, the results similarly grouped, are as follows —

## MONKEY

Animal	Cord divided at	Effect in sciatic nerve following							
		Excitation of posterior column of same side		Excitation of posterior column of opposite side		Excitation of lateral column of same side		Excitation of lateral column of opposite side	
		Min	Max	Min	Max	Min	Max	Min	Max
Monkey (270)	8th dorsal	59		0		0		0	
		40	70	0	42	0	6	0	0
Monkey (280)	7th dorsal		190		10		2		
			192		2		2		
			135		33		80		0
Monkey (221)	10th dorsal		98		26		45		8
			50		15		6		12
			57		24		40		2
			102		10		20		3
Monkey (333)	10th dorsal	58	68	18	12	0	10	0	0
			106		37		25		0
			112		52		6		0
Monkey (368)	10th dorsal	55		16		4		0	
		58		2		0		0	
			38		6		30		0
			37		14		9		5
			20		8		23		0
Aggregate sum		270	1275	36	287	4	304	0	30
Average		54	91	7	21	—	22	0	25

It will be seen that with "minimal" excitation the average effect obtained in the sciatic nerve of the Monkey by the excitation of the posterior column of the same side was nearly eight times as great as that of the posterior column of the opposite side. A small effect was obtained once after excitation of the lateral column of the same side, otherwise these results are in complete harmony with those in the Cat.

With the stronger stimulus the average effects following excitation of the two posterior columns have the relation of nearly five to one, the larger being due to that of the posterior of the same side, and, as in the Cat, a marked effect follows the excitation of the lateral of the same side, this being equal to that evoked by stimulation of the posterior column of the opposite side.

Finally, if all the results in both animals are blended and we compare both the average effect and the highest deflection obtained in response to excitation of each of the columns, the comparison shows the following results.



## AVERAGE Nerve Effect produced by Cord Excitation (Cat and Monkey)

	Average	Highest
Posterior column, same side	80	192
"    "    opposite side	15	68
Lateral column, same side	9	80
"    "    opposite side	4	12
Total . . .	110	

The sum of the average effects produced by all the columns is 110; of this the posterior column on the side of the nerve is capable of evoking about 73 per cent, the posterior column of the opposite side 15 per cent, the lateral column of the same side 9 per cent, and the lateral column of the opposite side 3 per cent.

There is a great similarity, at least as regards the relation of the crossed to the uncrossed side, between these different quantities and those which were referred to at the end of the nerve-to-cord experiments, detailed in Chapter IX. An exact similarity could not be expected, since we are dealing in the present case with mixed nerves, hence efferent as well as afferent fibres are the subject of observation

The presence of impulses which may be supposed to emerge from the cord by the anterior roots might account for an increase in the effect evoked in the nerves, since the excitation of such columns as the posterior may awaken reflex discharges from the cord down the motor roots

This explanation, however, cannot be applied to the effects evoked by excitation of the lateral column on the side of the nerve, since we see that the effect evoked by this column is smaller than that which the results of Chapter IX. would lead us to expect as probable from the indirect connections of its fibres with those of the posterior root only. There is no evidence of any accession of nerve impulses through this excitation, but rather of a resistance to the passage of impulses from the cord through the lateral indirect path into the fibres of the mixed nerve

It is, however, essential to ascertain the amount of the effects in the afferent and efferent nerve tracts before proceeding to discuss in more detail what the above experiments seem to indicate as to the relations of the cord to its nerves

#### SECTION 4.—THE ELECTRICAL EFFECTS IN AFFERENT NERVES FOLLOWING EXCITATION OF THE SPINAL CORD ABOVE THEIR POINT OF ENTRY

##### (1) *The Posterior Roots.*

The simplest mode of obtaining the effects in afferent nerves is that of exposing a posterior root, dividing it near the ganglion and connecting its cut central end and

the surface immediately above with the galvanometer circuit in the manner described. The objections to this experiment consist in the great shock to the animal which the necessarily prolonged exposure of the roots necessitated by the procedure seems to cause, and in the fact that the posterior root does not hold out as long as the sciatic nerve, its excitability being more readily influenced by falling temperature, drying, &c

We have however succeeded in three different animals (Cat) in obtaining a series of readings of the value of the root effect, the details of the experiments being as follows —

In all three animals, the left 7th lumbar posterior root was selected, this being the largest of the posterior roots in the Cat which receives afferent fibres from the sciatic nerve, as shown in the accompanying reproduction of a photograph of the plexus (See fig 18)

Fig 18



The cord was first exposed in the lower dorsal region and prepared for excitation at the level indicated in the table, and then the cauda equina, and thus the roots, laid bare. The 7th lumbar root was then exposed from origin to ganglion, ligatured near the ganglion and divided. It was raised in air by the ligature, and cables placed round its ligatured cut end and its surface 1 centim. above. The roots, as stated in Chapter IV, were remarkable in exhibiting a comparatively large resting electromotive difference between the surface and the cut section.

The different columns of the cord were then excited, first with "minimal" and then with maximal stimulation; it was found that the electrical effect in the root resembled

that of the nerve in character, but owing to the difficulty of keeping the root protected, and at the same time insulated, the amount of the effect, and, presumably, the excitability of the root, declined, especially in one Cat (341), the results, therefore, are all modified by the fact, that as the 'minimal' stimulus was applied first, the deflection caused by the excitatory electrical root change is much larger in the case of the "minimal" stimulus relatively to that of the "maximal" stimulus than would otherwise be the case.

The following table gives the results of the galvanometric observations, each deflection being produced by electrical changes in the nerve root, corresponding to the localised excitation, for five seconds, with the interrupted induction current of the sectional area of a special tract of the cord as indicated below.

EFFECT in Left 7th Lumbar Posterior Root

Animal.	Cord excited at level of	Excitation of left posterior column		Excitation of right posterior column		Excitation of left lateral column		Excitation of right lateral column	
		Min	Max	Min.	Max	Min	Max.	Min	Max
Cat (341) .	12th dorsal	190		9		0		0	
		135		6		0		0	
			110		32		0		0
			108		19		0		0
			90		50		0		0
Cat (348) . . .	11th dorsal .		90		45		10		0
		192		2		0		0	
		170		2		0		0	
Cat (362) . .	10th dorsal		200		70		0		0
		50		2		0		0	
			240		45		0		0
			253		15		0		0
Total sum . .	. . .	735	1091	21	276	0	10	0	0
Average	. .	147	156	4	39	0	—	0	0

It is seen that with the minimal stimulus an effect is practically only evoked by excitation of the posterior column of the same side as the root, with a stimulus of greater intensity an effect is also obtained with stimulation of the posterior column of the opposite side, this being one-fourth the amount of that evoked by stimulation of the column of the same side. As regards the lateral columns, only once was any effect in the root obtained, and that was with stimulation of the column of the same side.

If it be remembered that the minimal effect is exaggerated in the case of the posterior columns by the fact that their stimulation coincided with the fresh condition of the root, it will be seen that as far as the relations between the effects due to

excitation of the two posterior columns are concerned, the above experiments give results which are fundamentally the same as those obtained in the mixed nerve. On the other hand, the lateral column effect is almost entirely wanting in these experiments. The alterations in the excitability of the posterior root itself may be to some extent responsible for this, and in any case should, if possible, be excluded. In order to carry out this exclusion, experiments were performed in which, whilst investigating the effect in the mixed sciatic nerve, the (motor) efferent paths were annulled by section of all the anterior roots of the lumbar plexus.

(2) *Effects in the Sciatic Nerve after Section of Anterior Roots*

This experiment we have performed on two animals (Cats), in each of which the cord was divided and exposed for excitation at the level of the 11th dorsal vertebra, and the left sciatic nerve prepared in the usual way for connection with the electrodes. The lower lumbar cord and the cauda equina were then exposed in each animal by opening the canal for about 5 centims. The anterior roots of the left 5th, 6th, and 7th lumbar, and 1st and 2nd sacral nerves, were cut within the canal. All other connections were then divided, so as to leave the left sciatic nerve in connection with the cord by the posterior roots only.

The excitation of the cord proceeded in the usual manner, but a "maximal" intensity of stimulus alone was employed, and the time of stimulation was 7 seconds.

EFFECT in Left Sciatic Nerve after Division of its Anterior Roots.

Animal	Cord divided at	Excitation of left posterior column	Excitation of left lateral column	Excitation of right posterior column	Excitation of right lateral column
Cat (209)	11th Dorsal	125 130 85 92	not observed 50 not observed "	9 35 15 not observed	0 0 not observed "
Sum		432	50	59	0
Average		108	50	20	0

From these figures it will be seen that the effect evoked in the sciatic nerve by excitation of the posterior column on the same side was more than twice as large as that resulting from excitation of the posterior on the opposite side and more than four times as large as that due to the lateral on the same side.

In another animal the same anterior roots were divided, and in addition all the posterior roots on the left side and all nervous connections except the 7th lumbar posterior root, thus leaving the left sciatic nerve as a mere continuation of this

7th lumbar posterior root. Effects of 35 and 20 were obtained from excitation of the posterior column on the same side, and an effect of 10 with excitation of the posterior column of the opposite side, no effect followed the excitation of the laterals. This experiment is very difficult in execution, owing to the depressing effect which the severe character of the operation produces in the cord, both directly and indirectly, through shock to the animal. We have tried the experiment several times without success. As far as they go, the results of the second experiment would seem to indicate that the lateral column effect is not present when only one channel of influence, that of the 7th lumbar posterior root, is present, and this result is in accordance with the observations made upon the posterior root itself. It is not impossible that the results of the first experiments with the sciatic nerve given in Section 3, in which an effect was always obtained from the lateral column of the same side, are due to the fact that the nerve investigated was left in connection with the cord by fibres emerging from at least three posterior roots, beside the 7th lumbar, but as we have not been able to carry the investigation of this point further at present, we would merely emphasize the fact that the anatomical connections with the cord were different in the two cases.

### (3) *Summary of the Facts in (1) and (2)*

If now we sum up the results of all these experiments when the nerve investigated is connected with the cord by afferent tracts only, we find that the average effect evoked by excitation of the posterior column of the same side

$$= \frac{147 + 156 + 108 + 28}{4} = \frac{439}{4} = 110,$$

the posterior column of the opposite side

$$= \frac{4 + 39 + 50 + 10}{4} = \frac{103}{4} = 26,$$

the lateral column of the same side

$$= \frac{10 + 20}{2} = \frac{30}{2} = 15,$$

the lateral column of the opposite side = 0.

That is to say, as far as these readings go, of the sum of all the effects obtained, the posterior column of the same side was concerned with  $110/151 = 72$  per cent. of the effect in the nerve;

The posterior column of the opposite side was concerned with  $26/151 = 17$  per cent. of such effect;

The lateral column of the same side with  $15/151 = 10$  per cent. of the effect;

The lateral column of the opposite side with no part of the effect

It is most remarkable how nearly these average figures resemble those obtained by exactly similar average methods when the whole mixed nerve was the part investigated

This similarity suggested to us the possibility that the fibres in the anterior roots are but slightly concerned in the production of the electrical effect in the mixed nerve when the cord is excited by such strengths of stimulus as have been used in the foregoing experiments (500–2000, very rarely 4000)

It will be found on referring to Chapter VI, that whereas the electrical effect observed in the cord to follow excitation of the cortex is very considerable, it is very small in the sciatic nerve, and we there suggest that this difference involves a change in the amount, intensity, or quality of the nerve impulses in their passage through the unknown endings of the pyramidal tracts, and the known origins of the efferent nerves, the anterior cornual corpuscles (See fig 22, p 495, Chapter XI)

To what extent, and under what circumstances, electrical effects can be detected in the sciatic nerve, when all the posterior roots are divided and the nerve is connected with the cord by efferent fibres only in the anterior roots, becomes therefore a most interesting question

To the consideration of experiments upon this point we will now turn.

#### SECTION 5 --THE ELECTRICAL EFFECTS IN EFFERENT NERVES FOLLOWING EXCITATION OF THE SPINAL CORD

The least complicated mode of experimentation for determining these effects would be that of directly observing the changes in the central end of a divided anterior root. This experiment, however, we have not yet successfully accomplished, the difficulties in the way of obtaining satisfactory connections with a divided anterior root are augmented by its anatomical relations, and by the fact that, in order, as we shall see, to obtain any changes in the root an intensity of stimulus has to be applied to the cord which evokes general movements, thus dragging on the short root. The dangers of inadequate isolation have been already dwelt upon in Chapter IV. Our attempts in this direction were so unsuccessful that we determined to employ the more laborious method of division of all the posterior roots, and examination of the electrical changes in the sciatic nerve.

The plan of experiment, therefore, consisted in exposing the lumbar cord and cauda equina (see Plates 34 and 35, and fig 18), and then dividing the posterior roots of the 4th, 5th, 6th, 7th lumbar, 1st and 2nd sacral nerves, so as to leave the sciatic connected with the cord by the efferent fibres only

We made experiments upon seven animals (Cats) on these lines, but in two of these we unfortunately did not divide the 5th lumbar posterior root and the connection

with the 4th, which, as the figure of the plexus shows, possibly furnish some, though a very small proportion, of the efferent fibres of the sciatic nerve

The results of these two experiments are, therefore, not completely to the point, but they are interesting as showing the increase in the relative size of the effects obtained with excitation of the posterior column on the opposite side of the nerve, and of the lateral column on the same side, in comparison with those evoked from the posterior column of the same side.

The section of these posterior roots has thus cut down the preponderating effect obtained with excitation of the direct fibres in the posterior column

#### ELECTRICAL Changes in the Sciatic Nerve after Section of the 6th and 7th Lumbar and 1st Sacral Posterior Roots on the Left Side

	Intensity of stimulation	Effect in nerve following excitation of			
		Posterior columns same side	Posterior columns opposite side	Lateral columns same side	Lateral columns opposite side
Cat (204)	1000	58	70	40	0
Cat (207)		85	120	45	0
	2000	30	5	2	0
	4000	110	43	12	0
		11	25		
		294	263	99	
	Average .	59	53	25	

The excitation of the anterior columns produced no effect.

The results are, however, probably mixed, as will be seen by reference to the experiment on the remaining animals.

In these all connections of the sciatic nerve with the cord, except the anterior roots, were divided; the interesting fact then came to light that, even with a strength of stimulus above that employed in the previous experiments, very small electrical effects were evoked in the nerve by cord excitation, these being evoked by stimulation of the posterior column of the same side and the lateral of the same side. When, however, the strength of stimulus was increased very markedly, effects were produced which were more marked in the case of the lateral. It is not, therefore, until the intensity of the stimulus is far beyond the limits hitherto used that any marked nerve effect is produced by the passage of impulses from the cord down efferent nerve fibres.

This is illustrated by the following experiment upon a Cat (209), the cord being cut at the 11th dorsal, and all the posterior roots on the right side divided as



described. With a stimulus of 2000, effects in the right sciatic nerve were observed only from excitation of the posterior and lateral columns of the same side, the deflections amounting to an average of 10 only. On increasing the stimulus to a considerable strength (4000) a deflection of 70 was produced by the excitation of the lateral column of the same side.

Still more striking experiments are the following made upon two animals (Cats), which may be set out in detail, the necessary strength of the stimulus employed being noteworthy.

#### EFFECT in Efferent Nerves following Excitation of Spinal Cord.

Animal	Cord cut at	Strength of stimulus	Excitation of posterior column of same side	Excitation of posterior column of opposite side	Excitation of lateral column of same side	Excitation of lateral column of opposite side
Cat (195)	13th dorsal vertebra	4000	0	0	6	0
		8000	10	17	50	2
			2		32	
Cat (191)	10th dorsal vertebra	4000	12	0	18	
			6	0	35	
		5000	14	0	40	
		6000	12		60	
			30		40	
			15	0	36	
	Fresh section 11th dorsal	5000	28		35	
		6000	11		45	
			9	6	56	0

In the preceding experiments with afferent fibres, the maximal intensity of the stimulus was that represented by 2000; the great increase in the intensity of the cord stimulus necessary to evoke effects in the nerve through efferent fibres is, therefore, very striking.

Another animal (Cat) which was experimented upon in the same way, must be considered as furnishing rather doubtful evidence, since we had previously not only exposed and excited the cut ends of the various divided posterior roots on the side of the nerve in order to obtain reflex effects, but had divided all the anterior roots on the opposite side of the cord. These operations must, from their severity and extent, have altered the excitability of the cord itself. As far as they go, however, the results are in accordance with those just set forth, since a stimulus of considerable intensity (3000) was necessary to evoke any effect in the nerve which, in the case of excitation of both posterior columns amounted to 30, and in that of the lateral column of the same side to 36.

Finally, in order to avoid the changes in excitability following immediate section of the posterior roots, those belonging to the 5th, 6th, 7th lumbar, and 1st sacral nerves, were divided on the left side in a Cat (227) 26 days before the experiment. When

examined at this later date, the animal was found to move in an ataxic manner, but was not paretic; the sensibility of the left hind limb was very much diminished, and the left knee jerk was absent.

The histological examination of the cord showed at the lesion on the left side degeneration of (*a*) fibres entering the posterior cornu, (*b*) fibres in the posterior cornu, (*c*) fibres in the posterior root zone, (*d*) fibres in the posterior external column. Higher up, at the 11th dorsal vertebra, there was no degeneration in the entering fibres, but a large cornu-shaped patch of degeneration in the left posterior external column. The left posterior median column showed no definite degeneration until the lower cervical region was reached.

The experimental results were obtained by dividing the cord at the level of the 10th dorsal vertebra, and preparing both sciatic nerves for connection with the galvanometer. Each nerve when excited evoked electrical changes in the observed region, the left one (on side of lesion) more than the right. On stimulating the columns of the cord, and observing the effect on the left nerve, it was found that, with the ordinary strength of stimulus, very slight effects of 4 and 8 followed excitation of the posterior column of the same side, and no effects were obtained with this strength of stimulus from either the lateral of the same side or the columns of the opposite side.

On the other hand, in the right nerve, effects of 35 and 56 were evoked by stimulation of the right posterior, and varied effects from 2 to 65 on stimulation of the right lateral.

The observation could not be repeated with stronger stimulus owing to the failure of the animal.

An examination of all these results and comparison with those of Sections 3 and 4, will show that the effects aroused in the mixed nerve by stimulation of the spinal cord must be mainly due to nerve impulses travelling from the cord down the afferent (sensory) fibres; since the effect due to impulses travelling down exclusively efferent (motor) fibres, in the first place, is very small in amount and, in the second place, is only produced by a strength of stimulus in excess of that employed in the experiments on the mixed nerve, and finally, is then mainly evoked by stimulation of the lateral tract of the same side as the nerve under observation.

#### SECTION 6.—THE INFLUENCE UPON THE ELECTRICAL EFFECT IN THE NERVE OF INTERVENING SECTIONS IN THE CORD.

The experimental results to be studied under this heading throw more light upon the relations of the sciatic nerves to the spinal cord.

In the foregoing three groups of experiments, whilst excitatory electrical effects were evoked in the afferent, efferent, and mixed nerves by stimulation of the different columns in the cord, no direct evidence was afforded of the nature of the path in the cord along which the impulses, starting from the excited cross section

of any one particular column, pass to reach the nerve roots. It cannot be assumed that the result of the excitation of any particular column is to evoke nerve impulses which, in their passage to the issuing nerve roots, are limited to fibres in this particular column, or that any particular excitation, however strictly localised, may not excite by commissural fibres a neighbouring column. Indeed, as far as the cord itself is concerned, the evidence afforded by the experiments (Chapter VIII) shows there is no absolute limitation of descending impulses to one column.

It is, therefore, a matter of great importance in connection with the present investigation to ascertain to what extent in the foregoing experiments the path of such impulses as issue by the nerve roots is limited in the cord to the particular column stimulated. We endeavoured to obtain information as to this in the following manner: we first made experiments with the mixed nerve precisely similar to those already described (Section 3), that is, we connected the nerve with the galvanometer circuit, and excited the cut ends of the various columns of the cord, as displayed in a transverse section. We then made a section of one column between the seat of excitation and the lumbar roots of the sciatic nerve, and repeated the first experiment under these conditions. We were thus enabled to ascertain how far the nerve effect due to the excitation of any particular column was reduced when the fibres of that column were all cut through. Any remaining effect might be due to—

(a) The presence of fibres which passed from the stimulated into other columns;

(b) The presence of fibres connected with the corpuscular portion of the cord, and the awakening of the same by their means, the nervous impulses thus reflexly discharged proceeding either along fibres in other columns or along fibres in the same column below the interruption.

To what extent these various factors come into play will be made evident by a careful analysis of all the results. These are best grouped in accordance with the particular part of the cord which was the seat of the intervening section.

#### *A. Influence on the Effect in the Nerve of Hemisection of the Cord.*

The first group of results show that an intervening hemisection of the cord completely abolishes the nerve effect produced by excitation of the columns on the side of section, as well as that evoked by excitation of the posterior column of the opposite side.

Thus the spinal cord was exposed and divided in a Cat (329) at the level of the 9th dorsal vertebra, both sciatic nerves were now prepared for galvanometric observation, and the electrical effects obtained by exciting the cut section of the various columns at the 9th dorsal vertebra observed, the results being given as under.

Nerve observed	Column of cord excited			
	Excitation of left posterior	Excitation of left lateral	Excitation of right posterior	Excitation of right lateral
Left sciatic nerve observed, diff = 012 Daniell	Deflection 85	10	25	0
Right sciatic nerve observed, diff = 011 Daniell	„ 22	0	89	9
Hemisection of cord on left side at level of 1st lumbar vertebra				
Left nerve observed	Deflection 0	0	0	0
Right sciatic nerve observed	„ 5	0	130	8

The above experiment thus shows that with such an intensity of stimulus as that used (1000) the result of an intervening hemisection on the same side as the nerve is to abolish the nerve effect. If it is on the opposite side of the nerve, then the only effect interfered with is that evoked by the stimulation of the posterior column on the side of the lesion. It would therefore appear that with this strength of stimulus the nerve impulses, which subsequently cause the electrical effects, are localised to one side of the cord in both the area of stimulation and the subsequent path through the cord from that area to the issuing nerves.

There is, however, one point to which it is desirable to draw attention before proceeding to the next experiments. This is the absence of any effect in the left nerve when, with a hemisection limited to the left side, the right posterior column is stimulated. We do not interpret this as implying that there is no crossed path from the opposite posterior column to the roots of the lumbar nerves, but that either such crossing has to a great extent occurred at a higher level than the 1st lumbar vertebra, the level of the section, or that the hemisection had either directly (by injury) or indirectly lowered the excitability of the neighbouring posterior column, and that thus the intensity of stimulus used was inadequate to evoke nerve impulses which could pass down the afferent fibres of such an indirect path as connects this column with the nerves on the opposite side. This latter supposition is rendered not improbable by an experiment made upon an animal (Cat, 283)\* in which the hemisection had been performed four months before the experiment. The cord of this animal was exposed and divided for excitation at the 10th dorsal (the hemisection had been made on the left side at the 12th dorsal). The electrical effects produced in the two nerves by excitation of the different columns (coil 2000) were as follows —

\* For full description of this animal during life and after death see pp. 429-430.

	Excitation of left posterior	Left lateral	Right posterior	Right lateral
Cat (283)				
Left nerve , . . .	0	0	35	0
Right nerve	0	0	82	15

In this case the previous hemisection had rendered excitation of the columns on the side of the lesion quite ineffectual, as far as the generation and propagation of nerve impulses into either nerve were concerned. The excitation of the posterior column on the opposite side to the lesion, however, evoked effects in both nerves. It would, therefore, appear that the crossing through grey matter from the one posterior column to the other, and so to the nerves, was in this case below the level of the hemisection, viz, 12th dorsal vertebra. This experiment apparently is contradictory in its results, as regards the crossing from the opposite posterior column, to that just given, but putting aside the presence and absence of immediate shock in the two cases respectively, it must be remembered that the lesion in this case was two vertebrae higher up. The localisation to the particular column excited of the generated impulses at the area of stimulation is very clearly brought out by this experiment, as well as the failure of production of any crossed effect from the sound (right) lateral column into the left nerve.

*B. Influence on the Nerve Effect of Section of the Posterior Column on the Same Side as the Nerve Observed*

The influence of the section of one of the posterior columns will be here considered before that due to section of both, for although its effects are more complicated, the experimental procedure by which the changes were produced involved the section first of one and then of the other column. It will be found that the result is extremely definite as regards the particular column operated upon, as the following experiments upon two animals, Cat and Monkey, show. It will be noticed that a considerable intensity of stimulus was necessary to produce effects in the Monkey.

SECTION of one Posterior Column on the same side as the Nerve. Left Sciatic Nerve observed.

	Column of cord excited			
	Excitation of left posterior	Excitation of left lateral,	Excitation of right posterior	Excitation of right lateral
Cat (311)				
Cord divided at 9th dorsal vertebra				
Stimulus 500 . . .	130	0	20	0
	132	0	26	0
Left posterior column cut at 1st lumbar vertebra	0	0	10	0
Stimulus 500 . .	0	0	5	0
Monkey (333)				
10th dorsal .	106	25	39	2
Left posterior column cut at 12th dorsal vertebra				
Stimulus 4000 . .	3	18	12	2
	6	20	10	0

In these two cases an intervening section of the posterior column on the side of the nerve observed had the effect of entirely abolishing, or diminishing to a mere trace, the large nerve electrical change which was formerly produced by the excitation of that column. It may therefore be inferred, that the fibres which connect the posterior column at the level of the 10th dorsal vertebra with the posterior roots of the lumbar nerves on the same side, run wholly in that column, and that the stimulation and the path are strictly localised therein.

There is, however, a further result, that, namely, shown by a diminution in the nerve change evoked by stimulation of other columns. This may be due either to the cutting off of crossing fibres, or to a depressed condition in the excitability of the remaining part of the cord.

It is improbable, however, that both the latter causes operated in these cases, since when we group together in the next table the influence of the lesion upon the electrical changes in the nerve of the opposite side, although we obtain in both animals evidence of diminution, yet the condition of the Monkey after the section was evidently one of more and not less excitability than it was before, since the uninjured right posterior column evoked larger effects than it did in the normal state. (See Hyperexcitability after Section, Chapter IX., Section 7, C.)

*C. Influence of Section of the Posterior Column on the opposite side to the Nerve observed.*

RIGHT Nerve observed.

	Column of cord excited			
	Excitation of left posterior	Excitation of left lateral	Excitation of right posterior	Excitation of right lateral
Cat (311)				
Cord divided at 9th dorsal vertebra	36	0	108	0
Left posterior column cut at 1st lumbar vertebra	4 2	0	48 37	0
Monkey (333)				
Cord divided at 10th	52	4	112	15
Left posterior column divided at 12th dorsal vertebra	30	0	150	15

It is seen that the effect evoked in the nerve by stimulation of the posterior column of the opposite side is diminished by section. The diminution cannot be attributed to general lowering of excitability since it is present in both cases, and it will be seen that in the Monkey the excitability of other columns had increased. It must be due to the interruption by the lesion of fibres crossing through indirect channels from that posterior column. As this interruption occurs in the posterior column, it would imply that there are fibres which cross over from one posterior column to the other, which have a wide distribution along the cord. The diminution is due to the cutting off of such fibres as descend to cross below the level of the respective sections; the effect still obtained after the section may be due to those fibres which, having crossed above the level of the same, are not interrupted by the lesion. Reference to the spinal cord experiments (Chapter VIII.) will show that according to our experiments the fibres in the two posterior columns have very extensive indirect connections with each other.

*D. Influence of Section of both Posterior Columns on the Electrical Effects evoked in the Nerve.*

When both posterior columns were divided, mere traces of nerve effect were evoked by excitation of either column, even when the stimulus was sufficiently intense to produce marked effects from stimulation of the lateral column on the same side as the nerve.

This is shown by the following experiments made upon the same two animals, the nerve effect due to excitation of each different column being compared before and after the intervening section of the posteriors



Nerve observed	Column of cord excited			
	Excitation of left posterior	Excitation of left lateral	Excitation of right posterior	Excitation of right lateral
Cat (311)				
Section of 9th dorsal		Before	26	0
Left nerve (stimulus 500)	152	0	20	
	130		81	8
Right nerve	16	0		
Section of both posteriors at 1st lumbar		After	0	
Left nerve (stimulus 1000)	0	30	18	5
Right nerve	0	0	0	0
Left nerve (stimulus 2000)	0	65		
Monkey (333)				
Section at 10th dorsal		Before	112	6
Right nerve (stimulus 4000)	52	4		
Section of both posteriors at 12th dorsal		After	6	21
Right nerve (stimulus 4000)	6	0		
Cat (251)*				
Section, 1 month previous, at 10th dorsal				
Right nerve (stimulus 4000)	0	10	0	35

It is evident that the interruption, as far as the posterior column is concerned, is now practically complete for both nerves, hence all the fibres by which these columns are connected with the lumbar nerve roots are now severed, and thus any crossing of nerve impulses out of either posterior column into the lateral columns, or into any structure except the other posterior at a level higher than that of the 12th dorsal, is negatived.

It remains now to see the influence of section of the lateral column upon the effect.

#### *E. Influence of Section of the Lateral Columns on the Electrical Effects evoked in the Nerve.*

The limitation of the area of stimulation, and the localisation of the descending nerve impulses to the fibres of the excited column, are apparently very complete in the case of the lateral column, so far as the records of muscular movements can show. (*Cf.* SCHIFF, see p 347.)

It remains to be seen to what extent this is true of the particular impulses now studied which, as our previous remarks have shown, must be considered as conveyed into the nerve by the posterior as well as the anterior root fibres.

\* For full description of this animal, *i.e.*, appearances during life and death, see *ib.* 439

The experiments upon this point were made upon two Cats, in one of which (259)\* the lateral column had been divided 34 days previous to the experiment, whilst in the other an intervening section was made of all structures except one lateral column at the time of the experiment

The results of the experiment in the first case are given in the adjoining table —

LEFT Lateral Column divided 34 days before Experiment, at 10th Dorsal Vertebra

Nerve observed	Column of cord excited			
	Excitation of left posterior	Excitation of left lateral	Excitation of right posterior	Excitation of right lateral
Cat (259)				
Section at 4th dorsal vertebra				
Left sciatic observed—				
Stimulus 1000	35	0	0	0
	48	0	12	0
2000	22	0	52	0
Right sciatic observed—				
Stimulus 1000	20	0	40	0
2000	42	0	78	28

It will be noticed that no change at all in the left nerve followed excitation of the left lateral column, although, in the right nerve, a change was evoked from the right lateral column. Since, however, nerve effects are not easily evoked from the lateral column by moderate stimuli, and when these are employed strong violent reflex effects are produced by stimulating other columns, it was desirable to adopt a different procedure and make an intervening section of such character as would divide all fibres except those in one lateral column, which could then be used as a standard of comparison

The results before and after such division are shown in the following table —

\* For full description of this animal as regards its appearances during life and after death, see p 405

Nerve observed	Column of cord excited			
	Excitation of left posterior	Excitation of left lateral	Excitation of right posterior	Excitation of right lateral
Cat (363)				
Section at the 9th dorsal vertebra				
Left nerve				
Stimulus 500 . . .	42	0	8	0
1000 . . .	122	0	10	0
2000 . . .	138	0	28	0
Section of all columns except right lateral at 12th dorsal				
Stimulus 2000 . . .	0	0	0	0
4000 . . .	0	0	0	14
Right nerve Before section				
Stimulus 500 . . .	5	0	95	0
2000 . . .	28	0	145	0
Section of all columns except right lateral at 12th dorsal				
Stimulus 2000 . . .	0	0	0	0
4000 . . .	0	0	0	28

In these experiments, it is seen that the right lateral column was excluded from the section, and that stimulation of no other column above the section, except the right lateral, produced any nerve effect.

It has, however, been shown in Chapter IX that when impulses proceed up the posterior roots into the cord they are conveyed to some extent (20 per cent) by the lateral columns of the same side. A connection between the posterior root fibres and the lateral column, presumably by means of fibres in the posterior column or cornu, must therefore exist. This connection is, however, of such a special kind that it offers an evident resistance to the passage of impulses backwards from the cord into the root. The fact that no effects in the above experiment could be obtained when, with the lateral column as the sole bridge between the excited upper portion of the cord and the nerves, the posterior columns were excited, shows that any spread of path from the posterior to the lateral columns, if it exists, must either be below the level of the section (12th dorsal) or must offer a resistance to the passage of impulses in the downward direction which it does not offer to their passage in the upward direction, that is, in their ascent towards higher centres.

The relations which the cord columns appear to have with one another, as given in the summary of Chapter VIII., are in this respect of great interest and importance.

Two results are clearly brought out by the consideration of the series of experiments in the whole of this section; the first that the analogous character of the general electrical results in cord and nerve, without being pushed too far, may be extended to this point, that the stimulation of any one column in the cord is a localised stimulation of the nerve fibres in that column only, and the second, that the resulting nerve

impulses generated at the seat of stimulus are propagated to the root of the nerves along fibres constituting direct and indirect tracts, which are for the most part confined to the particular column which has been excited, the sole exception being that of the posterior column on the opposite side to that from which the nerve roots spring

### SECTION 7 — SUMMARY AND CONCLUSIONS

The experimental results detailed in this chapter form a sequel to those of the preceding Chapter IX., as to the relations which exist between the lumbar nerves and the spinal cord. Complete harmony between the results of the two series of experiments is not to be expected from the very different physiological and anatomical conditions which they involve. It will, however, be seen, if we compare the present results with those given in the summary of Chapter IX, that as regards the main points the one set form a corollary to the other.

In order that the salient features of the two should be clearly expressed, the following Table, in which all the results of the present chapter are massed under different heads, is laid before the reader

The Table shows the average percentage of the total amount of the effect which has been observed in the sciatic nerve, or its roots, when each lateral and posterior column of the cut cord is respectively stimulated

The same average percentage is also shown, when the stimulus is minimal, in a separate appended table

#### I — THE Amount per cent of the Total Nerve Effect evoked by adequate Cord Stimulation due to Localised Excitation of Particular Columns.

Character of nerve connected with galvanometer circuit	1 Excitation of posterior column of same side	2 Excitation of lateral column of same side	3. Excitation of posterior column of opposite side	4 Excitation of lateral column of opposite side
	Per cent	Per cent	Per cent	Per cent
Posterior root	85	3	12	0
Mixed nerve sciatic	73	9	15	3
Sciatic Nerve with anterior roots cut	73	10	17	0
Average	77	7	15	1

#### II — THE same when the Cord Stimulation is Minimal

Character of nerve connected with galvanometer circuit	1. Excitation of posterior column of same side	2 Excitation of lateral column of same side	3 Excitation of posterior column of opposite side.	4 Excitation of lateral column of opposite side
	Per cent	Per cent	Per cent	Per cent
Posterior root	97	0	3	0
Mixed nerve	84	0	16	0

If these results are to be relied upon as indicating not merely different amounts of electrical change, but the presence of different amounts of nerve impulses propagated from the stimulated area along the cord and into the observed nerve, then their main features indicate the following relations between the dorsal cord and the sciatic nerve in the case of *cord-to-nerve* experiments —

(1.) The path of least resistance, as shown by “minimal” stimulation, between the cord and the afferent fibres of the sciatic nerve, is that of the posterior column of the same side, this path being that of the directly continuous afferent fibres

(2) Of the indirect nerve paths between the cord and the afferent fibres, the path of least resistance is that of the posterior column of the opposite side, as is shown also by Table II.

(3.) The afferent paths, direct and indirect, along which nerve impulses can be made to travel (*backward*) from the stimulated cord to the sciatic nerve, have the following relations to the posterior roots of the sciatic nerve, as shown in Table I —

(a) The posterior column of the same side conveys 77 per cent of the amount of nerve impulses,

(b.) The lateral column of the same side conveys 7 per cent,

(c) The posterior column of the opposite side conveys 15 per cent,

(d) The lateral column of the opposite side conveys a mere trace.

We will now compare these deductions with those of the preceding chapter from *nerve-to-cord* experiments. These latter were briefly as follows —

(1) The spinal path by which afferent impulses proceeding up the nerve travel in the cord is, when these impulses are generated by “minimal” excitation, almost entirely that of the posterior column of the same side, *i.e.*, the directly continuous one.

(2) Of the indirect spinal paths along which such ascending impulses travel, that in the lateral column is the path of least resistance of the same side

(3.) All the afferent spinal paths have the following relations to the posterior roots of the sciatic nerves as regards the transmission of afferent impulses generated in the fibres of the sciatic nerve —

(a) The posterior column of the same side conveys an average of 60 per cent. of the total amount (intensity and quantity) of nerve impulses,

(b) The lateral column of the same side conveys 20 per cent,

(c) The posterior column of the opposite side conveys 15 per cent,

(d) The lateral column of the opposite side conveys 5 per cent

The following features of these two sets of deductions are similar —

i. That the channel of connection with the posterior roots is *par excellence* that of the fibres in the posterior column of the same side,

ii. That what crossing does exist is almost entirely due to indirect continuity with the fibres in the posterior column of the opposite side,

iii That the crossed path represents only about 15 per cent. of the available path;

iv. That the fibres in the lateral column have very much closer indirect relations

with the fibres of the posterior roots on the same side than they have with those on the opposite side, these last being scarcely represented

The most striking differences between all the connections of the posterior roots with the cord, as dependent upon whether impulses are made to ascend or descend them, are—

i For ascending impulses the lateral column of the same side affords indirect channels of *greater* efficiency than the crossed path in the opposite posterior column, or, *a fortiori*, the opposite lateral column

ii For impulses descending along afferent paths the lateral column affords indirect channels of *less* efficiency than the crossed path in the opposite posterior column

iii The ease with which the ascending impulses evoked by “*minimal*” excitation cross from the posterior root into the posterior column of the opposite side is considerable as compared with that which characterises the passage backwards from a posterior column into the opposite nerve roots when descending impulses are evoked by such “*minimal*” excitation

These differences tend to show that although there is no absolute block to the backward passage of impulses descending afferent channels into afferent fibres of the nerve, such as exists in the anterior roots to the passage upwards of ascending impulses in efferent channels, yet there is a physiological difference between the facilities which afferent indirect paths offer to the passage of impulses, this passage being much easier when it occurs in the normal ascending direction

We now consider ourselves warranted in concluding that, as far as the afferent tracts are concerned, the deductions of WOROSCHILOFF, MIESCHER, &c, referred to on p 420, are founded on experimental results which, from their nature, readily admitted of misinterpretation, and that both physiological experiment and anatomical investigation point with great distinctness to what is the true afferent path. Our observations confirm the views as to the physiological properties of the posterior columns set forth in 1847 by LONGET and reasserted by SCHIFF, with this modification, that although the posterior columns form the main path of connection between higher portions of the cord and the posterior roots of the nerves, yet there is a path in the lateral column which is strictly confined to the side of the entering roots

It may be urged that there are pathological cases (BROWN-SÉQUARD) which undoubtedly exist, of motor paralysis on one side and hemianæsthesia on the other, following a local lesion of the cord. In reply, we can only state that we believe much more definite evidence than that afforded by the existing clinical data must be forthcoming in order to shake the solidity of the foundations for our propositions, a solidity derived from the welding together of all the foregoing quantitative results of exact experiments. We therefore are compelled to regard the above clinical experiences as either in no way indicative of the normal relations of the cord to the nerves, or as capable of explanation on the supposition that the lesion has affected at the same time

the motor path (lateral column) on one side and the principal afferent path (posterior column) of the opposite side

Finally, the results of the foregoing sections have brought to light some interesting details as regards the relation of the cord to the efferent nerves

In the Table it will be noticed that the results, obtained with "minimal" stimuli, as regards the sciatic nerve, are not affected by section of its anterior roots, hence, as far as the cord stimulation in these experiments extended, no nerve impulses passed down the motor roots capable of causing perceptible electrical changes in the nerve except with strong stimuli.

As far, then, as the localisation of the path of efferent fibres in the cord is concerned, the present investigation has at present gained no further information, the lateral column on the same side as the issuing nerve is the main path for outgoing nerve impulses in the lumbar nerves. But the method has brought to light a remarkable characteristic of this path, namely, that at one portion, that which connects in the spinal nerve-centres the pyramidal nerve fibres with the origins of the anterior root-fibres, it exercises such a modifying influence upon the traversing impulses that these issue so altered in number, intensity, or quality, as to cause but very slight electrical effects in the nerves, and that it is not until a comparatively strong stimulus is used that the issuing impulses are of such kind as to cause really appreciable nerve effects.

This brings us to the subject of the next chapter, which deals with the physiological relations between the nerve-corpuscles and the nerve-fibres.

## CHAPTER XI—ON THE FUNCTIONAL ACTIVITY OF NERVE CENTRES AS EVIDENCED BY THE PRESENT METHOD

Section 1—The present state of knowledge of the relations of the nerve centres in the cord

(1) Anatomical (2) Physiological

Section 2—Experiments by the galvanometric method directly bearing on the spinal nerve centres.

1 Resistance offered by the efferent side of the centre to the passage of impulses

2 Resistance offered by the afferent side to the passage of impulses

Section 3.—Character of the impulses discharged by the spinal centres

Section 4.—The influence exerted upon the electrical changes in a directly-excited nerve by its attachment to the spinal cord

Section 5—The spread of reflex discharges up and down the cord (internuncial fibres)

Section 6.—On the electrical changes in the cortical nerve centres

Section 7—Summary

### SECTION 1.—THE PRESENT STATE OF KNOWLEDGE AS TO THE RELATIONS OF THE NERVE CENTRES IN THE SPINAL CORD.

The employment of the galvanometric method to estimate quantitatively the



excitatory state of the nerve channels or fibres in the cord led us to attempt to apply it as a gauge of the conditions prevailing in and between the spinal centres.

Even a careful review of the history of the subject fails to show absolutely more than a few facts from which knowledge of the actually intracentral processes may be drawn. We will now present in a brief sketch what is understood from anatomical and physiological evidence to fairly represent the structure and functional activity of simple nerve centres, such as those in the spinal cord, in order that the bearing of our own observations may be more comprehensible.

### 1. *Anatomical Relations*

The most recent anatomical investigations by GOLGI, HELD, FLECHSIG, and others, chiefly by means of the methods of staining devised by GOLGI, have established the justification for regarding a nerve centre in the spinal cord as constructed as follows —

- (a) An afferent side ("sensory"), to which run afferent channels from the posterior root
- (b) Field of conjunction between the afferent and efferent sides
- (c) An efferent side consisting of large nerve corpuscles, from which issue the efferent channels

(a) Examined in further detail it appears that, of the afferent channels running into the spinal cord from the posterior roots, some ascend directly in the posterior and postero-median columns, others enter the posterior cornu of grey matter, and are lost therein, others pass through the grey matter far into the anterior cornu of the same

Further, the afferent side is composed of a ground basis, fibres, and corpuscles, the branches of which cannot be traced soon after their subdivision

(b) The field or area in which connection exists between the two sides of a nerve centre is differently accounted for by various observers. All, however, are agreed that the central branches of the large efferent so-called motor corpuscles repeatedly subdivide towards the afferent side, and tend to form what was formerly described as a network (GERLACH), but the anastomosis of the elements of which appears to be more and more doubtful with further knowledge. (The actual mode of conjunction between the afferent side and these branches of the efferent corpuscles is, therefore, unknown; but it is easily conceivable that as much as is known, *i.e.*, subdivision, &c., may very properly be regarded as the seat of higher resistance, and we believe that this field of conjunction is the region in which should be localised what we subsequently express as the "block" to the passage of functional impulses.)

(c) The elements on the efferent side have been long known as the "motor" part of the nerve centres. The large corpuscles, recognised by many authors to be distinctly

fibrillated in their intimate structure,\* shew a peculiar arrangement of one medullated outgoing branch, and from the opposite side numerous subdividing branches.

*Spinal Ganglia*—A word must here be interpolated on the structure of the ganglion of the posterior root in its character as a simple nerve centre.

All research† on the anatomical structure of these ganglia goes to show that their corpuscles pass through a change in the course of their development, being at first bipolar and afterward unipolar, and that any axis cylinder in relation to any such corpuscle does not directly enter this but gives off a branch at right angles to the ganglion cell, thus forming what has been termed a T-shaped junction

In addition, it has been shown‡ that there are fibres (as “determined” by the degeneration method) which pass through the ganglion (spinal) into the posterior root without coming into any relation with its cells To sum up shortly, therefore, it is evident that there are passing through a spinal ganglion numerous direct protoplasmic nerve channels

We have now to sketch further the afferent and efferent relations of the spinal nerve centres with the encephalon, with the other centres in the spinal cord, and with the periphery.

*Afferent Channels of Communication*—The afferent paths may advantageously be considered in reverse order to that just given

The afferent fibres in the posterior root are now known to have the following destinations as regards the spinal nerve centres —

1. Some pass the centres and, without communicating with them, enter the postero-external column and finally course up the postero-median column to the nucleus gracilis

2. Others enter CLARKE'S column where that is present

3. Others enter the posterior horn, and are lost in it

4. Others enter the posterior horn, but pass through it to enter the anterior horn

5. Some fibres bifurcate on their entry into the cord, one branch ascending and one descending; the branches end in a fine plexus in the grey matter (KOLLIKER)

The different fibres leaving the spinal nerve centre to connect with its neighbour have never received absolute anatomical demonstration, but from the results of physiological investigation their existence must be postulated.

The afferent fibres connecting the spinal nerve centres with the encephalon have been determined by the degeneration method to pass up the direct cerebellar and antero-lateral tracts and have been traced as far as the cerebellum and pons, but no further

\* See particularly MAX SCHULTZE, and H SCHULTZE, 'Archiv f Anat. u. Physiol' FLEMMING HENLE'S 'Festschrift'

† See particularly RANVIER, 'Traité Technique d'Histologie' HIS, 'Tageblatt der Naturforscherversammlung zu Berlin, 1886' FRITSCH, 'Archiv f Mikrosk Anat,' vol 27, 1886

‡ MAX JOSEPH, 'Archiv f Anat u Physiol' (DU BOIS-REYMOND), 1887, p. 307

*Efferent Channels of Communication* —The efferent path from the encephalon, *i.e.*, cerebrum, is well known as the pyramidal tract, and the fibres composing it are commonly supposed to end in the corpuscles of the anterior horns. As this connection is of the utmost importance, we may be permitted to discuss the point at a little further length.

The evidence by the degeneration method shows that the principal mass of the pyramidal tract fibres do not run towards the corpuscular elements in the anterior or ventral horn, but towards the *posterior* or dorsal portion of the nerve centres, thus suggesting that the fibres join rather the field of conjunction than the efferent side. Again, the degeneration method shows clearly that no pyramidal fibres pass directly out into the anterior root.

Anatomically therefore there is evidence of some structural change in the path where the pyramidal fibre comes into relation with the spinal centres.

The distribution of the pyramidal fibres in the spinal cord is still so much a matter *sub judice*, especially after recent work by the histological\* methods, that the complete destination of the fibres, when yet at the upper part of the cord, is unknown.

The existence of efferent fibres (internuncial) connecting each nerve centre with the next and others below it have, like the afferent internuncial system, been surmised to exist from physiological evidence, all anatomical facts being wanting.

We believe that our previous experiments (see bilaterality, &c.) go to show that such efferent internuncial fibres must be few in number and but feebly differentiated.

The efferent channels from the spinal nerve centres are the fibres composing the anterior roots.

*Commissural Channels of Communication* —Of commissural connection between spinal nerve centres of opposite sides of the cord no certain anatomical proof exists, but the presence of such connection is surmised from the physiological evidence, and is morphologically suggested by many researches, especially those of LOCKHART CLARKE and GOLGI.

## 2 *Physiology.*

While the spinal nerve centres have been investigated in numerous ways since WUNDT† estimated the delay in the passage of an impulse through them, it is remarkable how little is known with certainty of their functional activity.

By the galvanometric method we have been able to establish some fundamental considerations on this matter, and, to indicate their bearing, we will first enumerate categorically the facts that have been previously ascertained by various investigators.

The facts may be conveniently divided under the headings of—

\* See particularly C. GOLGI, 'Anatomischer Anzeiger,' 1890, Nos 13 and 14, and C. SHERRINGTON, 'Journal of Physiology,' &c.

† WUNDT, 'Untersuchungen zur Mechanik der Nerven und Nervencentren,' 1876.

- A. Spinal ganglion.
- B Jugular ganglion of vagus
- C Spinal cord nerve centres
- D Channels of communication

A Owing to the fact that the spinal ganglion has been made the object of some important experimental observations we think it better to state these first, although they are not, in our opinion, to be placed on the same ground as the phenomena relating to the spinal nerve centres.

This latter position is justified on consideration of the anatomical structure of a spinal ganglion previously given, which shows that it is traversed by "through" protoplasmic channels

(a) *Transmission of the Excitatory Electrical Change.*

Du Bois-Reymond observed\* that when excitation was applied on the proximal side of a spinal ganglion the "negative variation" was observable in the nerve trunk on the distal side

(b) *Delay in the Transmission of a Nerve Impulse through a Spinal Ganglion*

Exner† considered that his observations on a spinal ganglion in the Frog, warranted the opinion that the delay in the transmission of the excitatory condition (negative variation) through a ganglion was the same as would be produced by its passage along a nerve fibre; that, in short, there was no special delay. As these observations were made with Bernstein's differential Rheotome, we agree with Gad that they may be possibly conditioned by summation.

(c.) *Trophism.*

As is well known since Waller's‡ classical experiments, the ganglion exercises a trophic influence on the afferent nerve channels§ running in the posterior root

B. Before passing to the observations on the spinal cord nerve centres, we must specially allude to the valuable work by Gad and Joseph|| on the subject of *delay* in a ganglion. The ganglion they chose was not a spinal ganglion, but its homologue, the jugular ganglion of the vagus in the Rabbit. By recording the instant of change in the respiratory movements when the vagus was excited, respectively on the proximal and

\* 'Untersuchungen über thierische Electricität,' 1849, vol 2, 5, 601

† 'Archiv für Anatomie und Physiologie —Phys. Abth.,' 1877, p 567

‡ 'Comptes Rendus de l'Académie des Sciences,' 1851, &c.

§ Excepting the fibres described by Max Joseph

|| 'Archiv für Anatomie u. Physiologie,' Du Bois-Reymond, 1888

distal sides of the ganglion, they established reason for believing that the impulses which affected respiration were delayed in transmission through the ganglion to the extent of 0.36 second. As GAD and JOSEPH point out, these experiments are open to the criticism that the summation of subminimal stimuli may be an important factor in producing the result.

C. The conditions under which the functional activity of the nerve centres of the spinal cord, as indicated by muscular contraction, is evoked necessarily form the major part of the facts at our disposal.

These conditions may be arranged as follows —

(1) *Adjuvants* — Warmth Preliminary influence of cold After effects of section of spinal cord\* a little distance above the nerve centre Some drugs, *e.g.*, strychnia, &c

(2) *Depressants* — Prolonged fall of temperature Shock after division of the spinal cord (greater in proportion to proximity of section to nerve centre)† Anaemia Narcotic drugs (anæsthetics, &c)

(3) *Delay* — A series of measurements have been taken of the time lost during the passage of a nerve impulse from one posterior root through a spinal nerve centre to the corresponding motor nerve of the same side. This delay, or time-loss, has been estimated by the majority of observers‡ to be about 0.1 in the Frog (EXNER, in man, bulbar reflex 0.4 second). This refers only to the “direct reflex,” *i.e.*, of the same side as the excitation.

The delay with the “crossed reflex” (see later paragraphs) is 0.04 second longer than the direct.

(4.) *Mode of Discharge* — A spinal cord nerve centre can be excited by a single induction shock if it be applied to an afferent channel. The effect produced as recorded by the contraction of a muscle is apparently that of a single twitch. If an interrupted current be applied to the spinal cord or an afferent channel, the effect similarly recorded is a continuous contraction.

An effect in the muscles of an intermediate form has been frequently recorded, *viz.*, a rhythm, the rate of which has been determined to be, on the average, eight to ten per second.

Occasionally an after effect has been noted, *i.e.*, a few muscular responses after the spinal excitation has ceased, and in some cases these are continuous.

(5) *Trophism* — It is well known that lesions of the spinal nerve centres which involve the efferent nerves are attended by wasting and other evidences of failure of nutrition in the parts which are in relation with the centre in question.

\* See FRANÇOIS FRANCK, *loc. cit.*, v. BEZOLD, *loc. cit.*, &c, &c.

† DE BOECK, ‘Archiv für die ges. Physiologie’ (confirmed also by our observations)

‡ Particularly HELMHOLTZ, WUNDT, FRANCK, CYON, and others *Loc. cit.*

(6) *Summation of Stimuli*.—A most characteristic feature of the functional activity of a nerve centre is its property of summing (STIRLING) subminimal stimuli with the effect of producing an apparently complete discharge

D The channel of communication between a spinal and other centres may be briefly alluded to as follows —

(a) *Relation of one spinal nerve centre to another*.—It is not possible on this point to improve upon the classical “Gesetze” of PFLÜGER,\* viz, that—

(1) In a simple reflex the muscular response is always on the same side as the excitation

(2) If a reflex is bilateral, the analogous muscles of the opposite side are thrown into action

(3) If a reflex is bilateral, the movements on the side opposite to that stimulated are much weaker than those on the same side (Cf our results on p 494)

(4.) If associated reflex centres are excited, the association is found to have an ascending arrangement in the spinal cord, culminating in the medulla oblongata, whereas of the encephalic reflexes the association is of a descending character, and also culminating in the bulb.

(b) *Conduction*.—SCHIFF† showed, by section of the crossed pyramidal tract, that the fibres running in it to the lowest spinal centres were undoubtedly the channels of conduction from the encephalon

EXNER‡ came to the conclusion, by time measurements, that there was a delay experienced by the excitatory condition or impulse traversing the spinal centres, when, the descending tracts in the cord having been excited, muscular contractions followed; but he admits that his results do not permit of a demonstration of the amount of time lost.

## SECTION 2.—EXPERIMENTS BY THE GALVANOMETRIC METHOD DIRECTLY BEARING UPON THE STRUCTURE OF NERVE CENTRES

### (1.) *Resistance offered by the Efferent Side of the Centre to the Passage of Impulses*

The results which have been obtained by our method are best arranged according to the particular part of a nerve centre to which they appear to refer

In considering the anatomical structure of a nerve centre as we have given it on p. 479, it is evident that the region of greatest obscurity is that which we have termed the area or field of conjunction between the afferent and efferent sides, and

\* ‘Die sensorischen Functionen des Rückenmarks der Wirbelthiere,’ v. E PFLÜGER. Berlin 1853

† ‘PFLÜGER, Archiv,’ vol. 30, 1883, p 248.

‡ ‘PFLÜGER, Archiv,’ vol. 8, 1874, p 537.

in which there is from physiological evidence reason to believe considerable delay occurs in the passage of the impulses through the centre

Such histological evidence as has been referred to in Section 1 suggests that the structure is of such nature as not to facilitate the passage of impulses through this region, but when we performed the following series of experiments we were surprised to find the degree to which such hypothetical obstruction really prevailed. It occurred to us that the obstruction might be more marked to excitatory impulses passing in the *reverse* direction, *i e*, from efferent to afferent mechanisms. We were not at all prepared, however, to discover, as we have done, that that obstruction was actually an absolute block, nevertheless, such appears to be the case.

To ascertain this we arranged the experiment as follows —

Having divided the cord at the level of the 10th dorsal vertebra (see fig 19), we raised its peripheral end for observation as described in previous pages and connected it with the galvanometer by its cross section and surface. The cauda equina having been exposed to an adequate degree, a pair of nerve roots was selected (usually the 7th lumbar), divided just above the intervertebral foramen and then central end raised in the air by ligatures and separated. The exciting electrodes were then applied respectively to the central ends of the posterior and anterior roots (see fig 19, *Ex p* and *Ex a*).

The excitation in the first case invariably evoked a large deflection of the galvanometer, but in the second case *absolutely nothing* even when the secondary coil was brought to 12500 of the Kronecker scale, thus completely covering the primary, *i e*, the zero point of the centimetre scale. In other words, the excitatory condition, arriving by the afferent channel or posterior root, not only passed up the few direct fibres of the postero-external, and later of the posterior median column, but probably aroused the afferent portion of the centre from which additional effects might ascend the cord by the internuncial fibres, thus producing a very large deflection in the galvanometer.

On the other hand, the excitatory condition which arrives at the nerve centre by passing up the anterior root or efferent channel is totally unable to reach the afferent side of the centre, and so ascend the cord.

The importance of the negative result of this experiment caused us to vary it as follows —

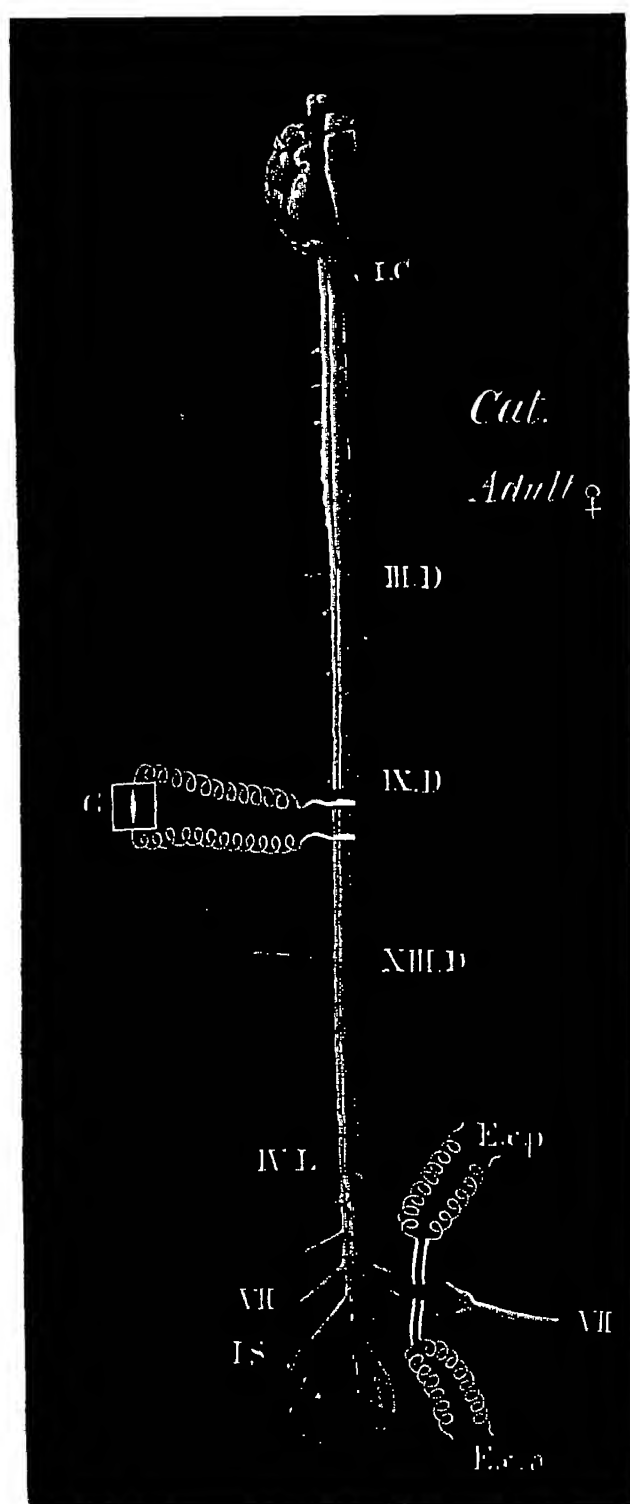
In two Cats we divided the posterior roots of the 4th, 5th, 6th, and 7th lumbar nerves and the 1st sacral on the left side. We then divided the cord in the lower dorsal region (10th dorsal), and connected the upper end of the lower fragment with the galvanometer. On exciting the left (mixed) sciatic nerve, which was in connection with the cord by the anterior roots only, no electrical change could be evoked in the observed region of cord however intense the stimulus used, whereas, excitation of only one opposite posterior root gave deflections of 350°, 320°, and with a stimulus of only 500, 130°. This method avoided any chance escape of stimulating current,



which, when this is very intense, might possibly occur in the case of the short anterior root

These experiments not only illustrate in a very striking manner the extent of the block to the passage of impulses backwards through the efferent side of a spinal

Fig 19



nerve centre, they also afford information upon the nature of the anatomical connections of the anterior root fibres with the cord. The histological enumerations of BURGE, the developmental researches of HIS, and the extent of descending degeneration in efferent tracts, have combined to indicate that all the fibres of the anterior roots are in connection with nerve cells lying in the immediate neighbourhood of their

attachment to the cord, and that there are no fibres which pass directly from the columns of the cord (above) outwards into the anterior roots without interruption in a nerve centre. If any uninterrupted fibres exist, then the excitation of the central end of an anterior root ought to give an effect in the galvanometer as arranged in this experiment, for it is well known that the excitatory state (*i. e.*, negative variation) travels indifferently in either direction along continuous tracts. The absence of such effect is a very convincing proof that such through fibres do not exist. Moreover, an additional point receives elucidation from this same experiment. We have already drawn attention to the fact that the anatomical relations of the pyramidal tract fibres are for the most part (and wholly as far as the lower limb is concerned) not with the efferent side of the spinal centres but rather with either the field of conjunction or the afferent aspect.

This anatomical juxtaposition of parts suggests to us that the pyramidal tract fibres for the lower limb do not immediately end in the efferent corpuscles. Such a conclusion is in harmony with the experimental results now under discussion, for it is unreasonable to suppose that the excitatory process would be so entirely blocked when proceeding in the reverse direction along a path consisting merely of two fibres (that of the anterior root and that of the pyramidal tract) joined by a large corpuscle such as one of those in the ventral (anterior) horn.

But we must not anticipate the facts which bear upon the mode of termination of the fibres of the pyramidal tract, and must return to the question of the block offered by the construction of a centre to the passage of nerve impulses.

## (2) *Resistance by the Afferent Side of a Nerve Centre to the Passage of Impulses*

After having discovered the fundamental position that it is impossible for an excitatory condition to pass "backwards" through a nerve centre from the efferent to the afferent side (whence it could easily spread up the cord), it was clear to us that the next point to be brought into relation with that just described would be the possibility of a nerve centre discharging its energy backwards down an afferent path; or in other words, whether the excitatory condition, if started in the afferent side of a nerve centre, could be transmitted backwards along the posterior roots. Upon this subject we have accumulated a number of facts and experiments from several points of view, and as these are in mutual agreement we can answer the question unhesitatingly in the affirmative.

Many of the facts which establish the conclusion that a spinal nerve centre can and does discharge energy down the posterior as well as the anterior roots when it is stimulated into activity have more important bearings on other questions raised in the present paper, and consequently have been referred to in Chapters VIII. and X. We will, therefore, simply enumerate the facts, and refer the reader to these chapters in which they are described, detailing only those which have not been already treated.

We reserve also to the end of this chapter the pertinent bearing of these observations upon the important doctrine of kinæsthesia (BASTIAN).

The evidence of the passage of nerve impulses, as indicated by electrical changes, from the aroused centres in the cord down the afferent (sensory) fibres of the posterior roots may be grouped as follows --

(1) Electrical changes in the posterior roots and mixed nerve with all anterior roots cut when the spinal centres discharge under the influence of strychnia

(2.) Electrical changes in the above structures when the spinal centres are discharged reflexly

(3) Electrical changes in the above structures when the spinal centres are aroused by electrical excitation of the columns of the cord.

(1) *The Electrical Changes in the Posterior Roots when the Spinal Centres are Excited by Strychnia*

The most remarkable illustrations of the fact that impulses emerge from a discharging spinal centre on its afferent as well as its efferent side, is that furnished by the following experiments

In a Cat (211) the cord was divided as usual in the lower dorsal region (11th dorsal) and both sciatic nerves exposed and divided. The central end of each nerve was connected when desired with the galvanometer. The cauda equina was then exposed, and the posterior roots of the 5th, 6th and 7th lumbar nerves, and those of the 1st and 2nd sacral, were divided on the right side, whilst the anterior roots of the same nerves were divided on the left side

The right nerve was thus in connection with the cord by its anterior roots only, the left by its posterior. Thirty minims of a 1 per cent. solution of acetate of strychnia was now injected intraperitoneally. When the tetanic strychnia spasms commenced, excitatory electrical effects were observed in both nerves

The amount of the deflections varied with the intensity and direction of the spasms, but were always larger in the right nerve (posterior roots cut) than in the left, averaging 180 in the right, and 30 in the left. The effect, though smaller in the posterior root, was absolutely definite in character, each spasm being accompanied by an effect.

In another animal, Cat (341), we divided the cord at the 12th dorsal vertebra and exposed the cauda equina. We then selected the 7th left lumbar posterior root, divided it near the ganglion and connected in accordance with our method the central end with the galvanometer

Thirty minims of a 1 per cent solution of acetate of strychnia were then injected into the peritoneal cavity. Each strychnia spasm caused excitatory electrical effects in the posterior root, which gradually increased in amount in proportion as the discharges became more violent and prolonged. The galvanometer deflections, which were very definite in character and similar in direction to those obtained by the passage of nerve impulses, amounted to 40 at first, then 70, and finally 120

The employment of clamps, &c, obviated any errors due to the movement of the animal, the experiment may, however, be objected to on the ground that the strychnia discharges are abnormally intense, and must thus break through resistances which ordinary central discharges would be unable to. That the centres can discharge down posterior roots without being under the influence of strychnia is, however, shown by the frequent occurrence of similar though smaller galvanometric effects in the posterior root of an unstrychnised animal, when the cord is discharging in consequence of previous electrical excitation and shallow narcosis.

(2) *The Electrical Changes in the Posterior Roots when the Spinal Centres are Discharged Reflexly.*

As in the preceding experiments, so here, the evidence is that derived from the electrical changes observed, (a) when the posterior root was directly connected with the galvanometer, and (b) when the (mixed) sciatic nerve was connected (after division of all anterior roots) with the galvanometer and the central end of one posterior root excited.

(a) In this experiment the central end of one divided posterior root was connected with the galvanometer and the sciatic nerve of the same side stimulated, the result being to produce in the galvanometer a deflection of 20 scale whenever the muscles were thrown into a full reflex spasm (coil 8000, 341). We shall see presently that this is the amount frequently obtained from the mixed nerve as the result of a reflex discharge. It is most interesting, therefore, to see that the centre reflexly discharges backwards down the posterior root. The bearing of this on the discussion as to which part of a centre is probably the source of the kinetic nerve will be seen further on when this question is raised.

(b) We varied the experiment in another animal, Cat (268), by dividing all the anterior roots supplying the left sciatic nerve and connecting the cut central end of this latter with the galvanometer. We then divided one posterior root, the 6th left lumbar, and excited its central end.

By this arrangement we obtained excitation of the spinal centres in the lumbar enlargement, and at the same time left only the posterior roots or afferent channels for any downward discharge such as would evoke electrical changes in the sciatic nerve.

One observation gave an effect of 10, another of 19 in the galvanometer, the reflex being weak in the first and fairly strong in the second.

(3) *Existence of Electrical Changes in the Posterior Roots when the Spinal Centres are aroused by Electrical Excitation of the Columns of the Cord.*

The details of these experiments, in which a posterior root was connected directly with the galvanometer and the cut surface of the spinal cord in the dorsal region excited,

are given in Chapter X. Reference to this Chapter will show that the effects in the posterior roots may be due to (a) conduction of nerve impulses from the excited area down directly continuous fibres, (b) conduction of nerve impulses down fibres which come into relation with cells, and only indirectly with the fibres in the roots. To these two must now be added (c) the discharge of impulses from the centres in the cord aroused by the excitation.

It is evident that the discrimination of these different factors can only be achieved by careful comparative experiments made upon the cord, when its direct connections with the roots having been interrupted, the centres are placed under different conditions as regards excitability. These experiments have not as yet been sufficiently satisfactory to enable us to form any decisive opinion on this point.

There is however, one very important fact already referred to at the close of the preceding Chapter X, to which we must now draw attention.

It will be remembered that, on comparing the results of the experiments detailed in Chapters IX and X. respectively, the inference was suggested that the indirect channels by which the cord communicates with the posterior roots, are of such a character that they offer more resistance to the passages of impulses from the cord to the nerve than to the passage of similarly evoked impulses from the nerve to the cord. There is thus evidence that, as regards these indirect channels, the same phenomenon of unequal conduction is present which, in its most marked form, exists in the case of the efferent region of the spinal centre.

It must, however, be borne in mind that these indirect channels do not necessarily form the afferent side of the centres, but are only in relation with them, since it is quite possible that in many instances these fibres pass through cells without entering that field of conjunction which forms the *terra incognita* of the centre. Evidence, therefore, of the nature of the discharge from this *terra incognita* backwards down the posterior roots, as well as forwards through the anterior cornual cells, could only be obtained through electrical excitation of the cord, if such excitation was limited to the pyramidal tract. The simplest way of performing this experiment is that of exciting the commencement of this tract in the cortex cerebri, and of observing the changes in the posterior roots. We have endeavoured in two animals to perform this experiment, but without obtaining as yet any satisfactory evidence, nor is this to be wondered at, when it is borne in mind how comparatively small the effects are in the mixed nerve under these conditions.

Summing up the evidence obtained from all methods of experimentation, we are led to conclude that when a spinal nerve centre is thrown into activity, a portion of its energy flows as a discharge backwards down the posterior roots as well as forwards down the efferent fibres of the anterior roots, and upwards and outwards along internuncial fibres to the next centres.

With this somewhat enlarged view of what occurs when a spinal nerve centre

discharges, we will proceed to show what fresh light the galvanometric method is able to throw on the character of the issuing impulses

### SECTION 3 — CHARACTER OF NERVE IMPULSES DISCHARGED BY THE SPINAL CENTRES

It seemed to us that an estimate of the amount of the impulses which pass along the nerves as the discharge of a reflex centre, might be obtained by comparing the amount of the electrical change in a peripheral nerve when (*a*) the centre is reflexly aroused, and (*b*) the nerve itself is subjected to a stimulus of similar duration and strength. Such an estimate can only give approximate results, but the difference revealed in the two cases is so striking, and the desired comparison of so much importance in attempting to analyse the components of a reflex, that we have devoted some time to securing it. We have done this for both a "simple" reflex, *i e*, that obtained from the same side as that of stimulation, and we have also measured the effect when it is the result of a "crossed" reflex.

#### (1) *The Excitatory Electromotive Change Produced in a Mixed Nerve when a Spinal Centre is Excited Reflexly.*

(*a.*) *Simple Reflex*—To obtain the electrical effect produced by a simple reflex discharge into the peripheral nerves, we divided the spinal cord in the dorsal region, then prepared and divided the sciatic nerve and connected its central end with the galvanometer. The cauda equina was exposed to a limited extent, and a posterior root of the same side selected for excitation, this was divided near the ganglion and its central end stimulated. (See fig. 20.)

The excitation was performed for a known time, as in all our experiments, and the galvanometric effect obtained in the nerve noted. We then applied the same, or a weaker stimulus of the same duration to the observed nerve. The results obtained form a remarkable contrast. The strength of the stimulus is so greatly altered in its effect by the condition of the animal, rest, depth of narcosis, &c, that what is minimal in one case, is quite adequate, or maximal in another.

The readings of the deflections indicating the reflex electrical effects in the nerve were :—

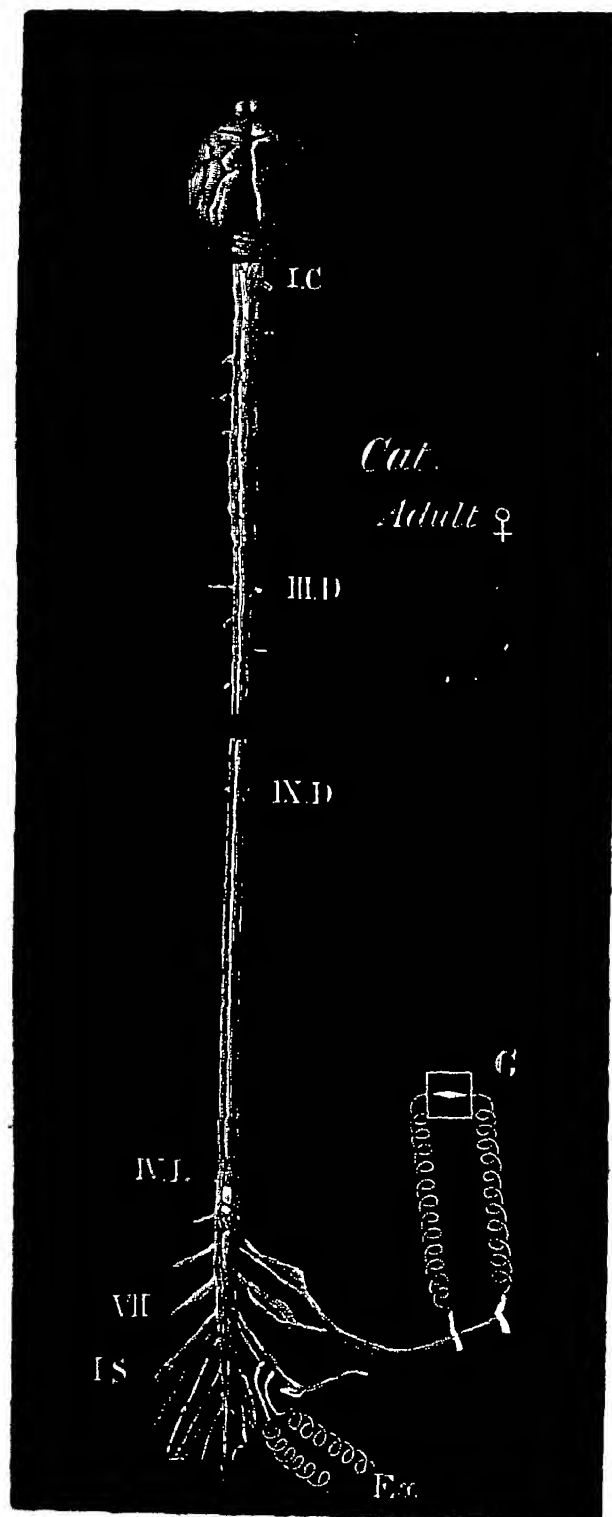
Highest readings	.	.	72	60	55	(three highest taken)
Average	.	.	26			
Lowest readings			7	3	nil	(three lowest taken).

Out of the whole number of observations, 9 per cent gave no result. Finally, the stimulus employed on the average amounted to 2500 of the inductorium scale.

Taking the average result, namely, 26 of the galvanometer scale, it is at once

obvious what an extraordinarily small reading this is when compared to that which is observed in a peripheral nerve, or even the peripheral portion of a divided posterior root, which, with a stimulus of one-fifth the intensity (500), and similar duration, averages 227 scale, and once reached a maximum of 445 scale

Fig 20



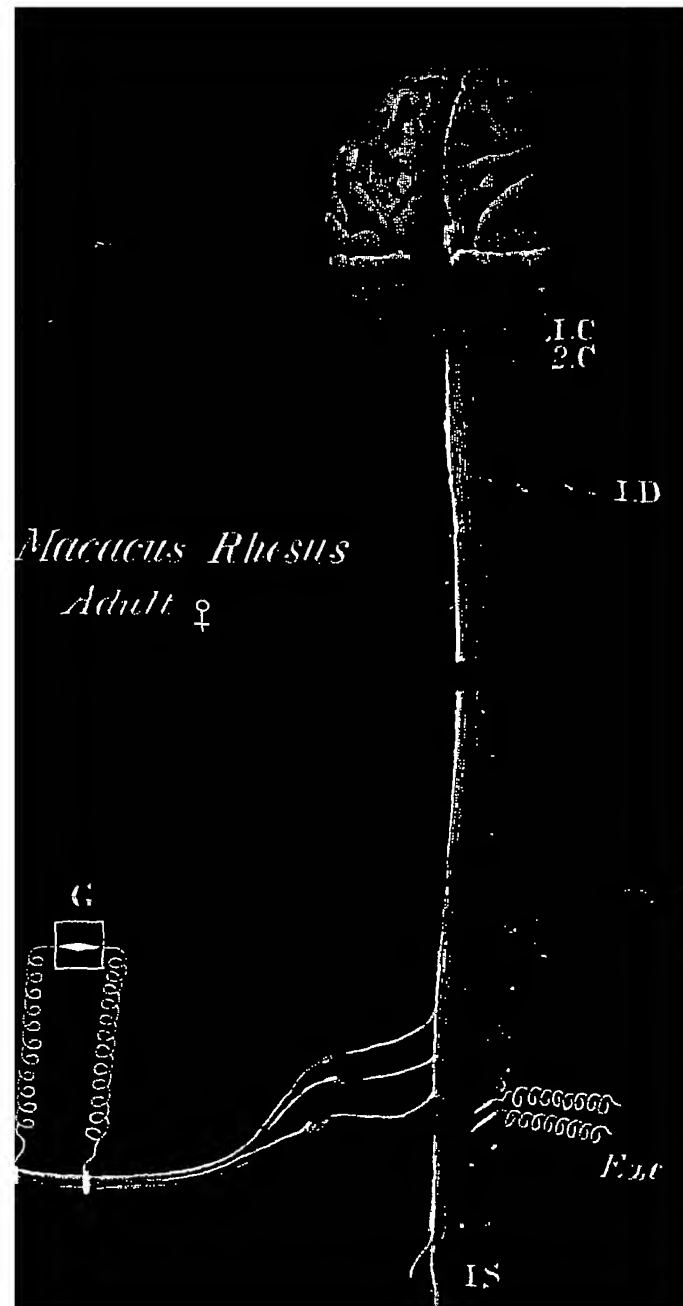
This definite result is very significant, but before enlarging upon it we will describe the values obtained for the "crossed" reflex

(b.) *Crossed Reflex*—To obtain the value of a crossed reflex discharge in the peripheral nerves, we divided, as before, the cord in the dorsal region, and then prepared one sciatic nerve for connection with the galvanometer, and next, either



the opposite sciatic nerve, or corresponding posterior root of the opposite side, for excitation. We made this experiment in nine Cats, two Monkeys, and one Rabbit.

Fig 21



The effect in the observed sciatic nerve was, consequently, that due to the discharge of the nerve centres on the side opposite to that of stimulation, or on both sides of the cord.

Owing to the higher excitability of the posterior roots, as compared with that of the mixed sciatic nerve, it is not surprising that we found considerable difference in the amount of effect obtained by crossed reflex action, according as it was

elicited by the one or the other of these two ways. We, therefore, separate the effects into two divisions indicating this difference

*Posterior Root* — The general results in this series of experiments were as follows. —

EFFECTS in nerve by excitation of opposite root.

Highest readings	45	42	42	(three highest taken)
Average	25			
Lowest readings	8	6	nil	(three lowest taken)

These figures are, on the whole, lower than those of the simple reflex. Other considerations emphasise this contrast. These are (1) the proportionate number of cases in which no effect occurred, this being, with the simple reflex, 9 per cent. of the total number of observations, but with the crossed reflex three times as much, viz., 27 per cent., (2) the average intensity of the stimulus required to evoke the effect, this being for a simple reflex, an intensity indicated by the secondary coil at 2500, for the crossed reflex the higher intensity indicated by the coil at 3500. Thus, as compared with the simple reflex, the crossed reflex is feebler, less often obtained, and when obtainable requiring a more pronounced stimulus applied to the afferent fibres in a posterior root.

*Sciatic Nerve* — In addition to the above we have observed crossed reflex effects which are not comparable with the simple uncrossed effects, since they were evoked by excitation, not of a root, but of the opposite sciatic nerve.

These effects are smaller and more difficult to elicit than those just indicated.

The effects were evoked and observed in precisely the same manner as in the previous cases, and the amounts of the deflections in the central end of the sciatic nerve were as follows: —

Highest readings	. . . . .	20	15	14 (three highest taken)
Average	. . . . .	10		
Lowest readings	. . . . .	6	5	

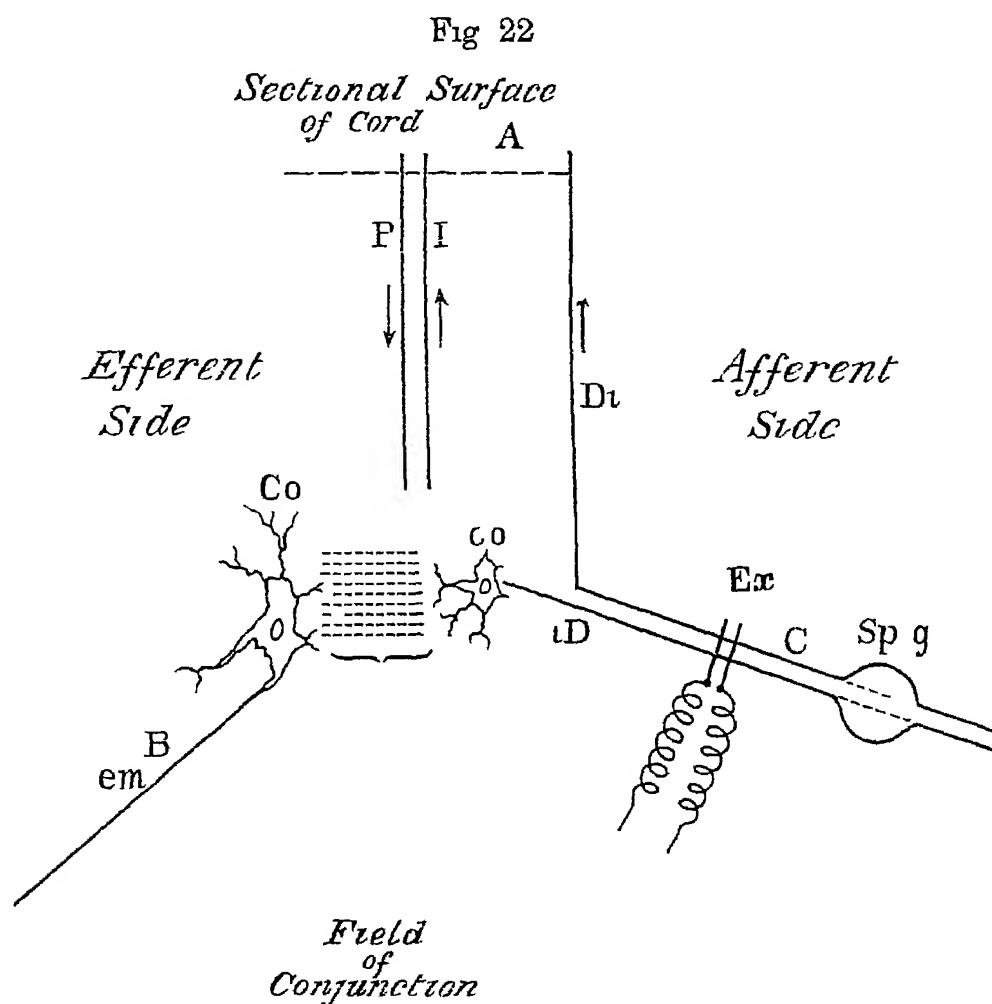
The intensity of stimulus required to evoke these effects was very much higher than in either of the previous instances, the average being represented by a position of the secondary coil of 8300, whilst it often happened that a position of 12,000 was necessary. It may be remarked that the use of the Helmholtz side-wire in the inductorium minimised any error due to electrotonic escape, such as produces the well-known phenomenon of the so-called "paradoxical contraction."

We are now in a position to consider the significance of these results.

The remarkable difference in quantity between the electrical effect in the nerve obtained by exciting the fibres themselves and that which is the result of a reflex discharge from the cord implies that, however intense the excitation of the afferent

side of a centre, the amount of the flow and the intensity of the processes which emerge from the efferent side is small. A comparatively intense excitation is necessary for the etherised centre to discharge at all, and the emerging impulses are so altered in their time relations and intensity, or limited to so few channels, that but little evidence of their presence is indicated by the galvanometric method

To facilitate further explanations we would call attention to the following diagram, fig 22, in which are represented the hypothetical elements of a nerve centre



In fig 22 are shown as simply as possible the three constituent parts of a simple nerve centre, namely, the afferent side, field of conjunction, and efferent side. In addition, the diagram represents the known part of the afferent channel which forms the direct ascending fibres in the spinal cord ( $D_1$ ), the internuncial fibres ( $I$ ), which also ascend, but which are not yet absolutely known, and the fibres of the pyramidal tract ( $P$ )

If a posterior root be excited at the point marked *Ex* in fig 22, we can obtain a record of the electrical change evoked by such excitation, in the following parts, namely, the portion of the cord (*A*) above the excitation, in the outgoing channel (*B*) (*em*), and in the channel of excitation (*C*). On taking the average of all such records we find that they are as follows —

Average at A	198.
„ B .	26.
„ C .	250.

Although the cross sectional area of the root is much smaller than that of the cord, yet the effect in the fibres of the root (C) is greater than that in the fibres of the cord (A), suggesting that there is less nerve energy after propagation through the afferent side of the centre. It seemed at first sight not improbable that the effect at A produced by the passage of nerve impulses up the direct channels which join A with C, plus additional nerve impulses evoked by a discharge of central activities, would be very large. It would seem, however, if the electrical indications are to be relied upon, and we see no reason to discredit them, that the impulses which enter the central structures from *Ex* suffer a diminution which more than counterbalances any such addition. We are, however, well aware that the reduction may be due to a spread of nerve impulses in their passage through the afferent side of a centre, and since a similar reduction occurs both in the case of impulses descending the pyramidal tracts, and emerging in the roots, as well as in those which as described are reflex in character, we incline to the opinion that ascending nerve impulses do suffer a diminution in intensity in their passage through the afferent side of a centre.

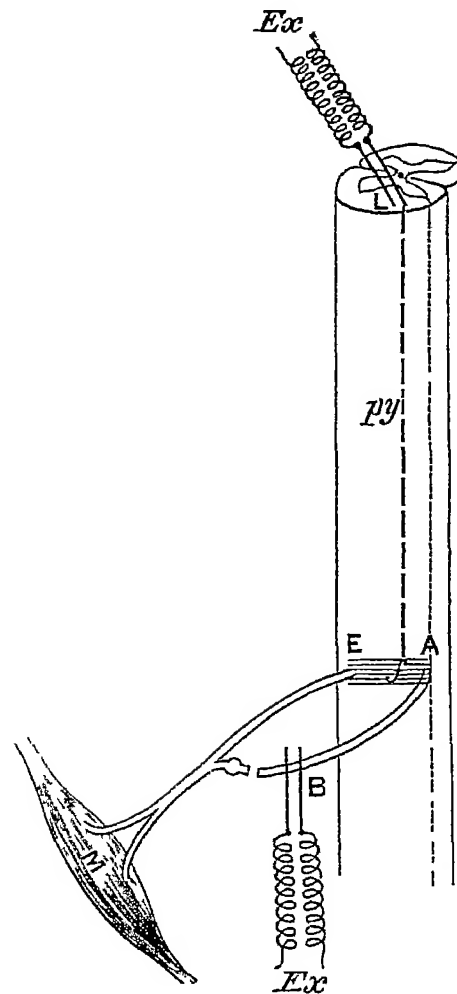
With reference to the impulses descending the pyramidal tracts, whether originating in the cortex cerebri or the fibres of the corona radiata, the facts given in Chapters V and VI suggest that a very considerable reduction occurs before they emerge in the anterior roots.

In this connection we would here draw attention to some experiments which we have made to record the muscular contraction evoked by excitation of the spinal centres, and particularly to measure the time between excitation and the commencement of the muscular contraction. The period of delay or latency thus estimated was ascertained by the use of TIGERSTEDT'S signal method, as described in Chapter III, Section 3, and in Chapter VIII., Section 1. In the latter place we have indicated at length the method we employed for the measurement of the rate of transmission of the excitatory effect in the cord fibres, which we found to be about 39.5 metres per second. We have now to point out the reasons which led us to measure the loss of time in a Mammalian spinal nerve centre. It appeared to us that this loss of time which the excitatory condition suffers in going through a spinal nerve centre would not be the same if the path of its entry into the centre is different. There are two modes of entry with which we are familiar. These are (1) the termination of the pyramidal fibres in the nerve centre, (2) the termination of the afferent channels in the posterior root in the nerve centre.

Now, as stated on p. 481, the latter has frequently been estimated, but EXNER has attempted the measurement of the former, and not with a very definite result. These periods of time have not to our knowledge been measured in the Cat, and, as we felt the importance of forming some idea of their value, we performed a few experiments as follows.

The problem in each case is shown in fig. 23. The nerve centre is at EA, E being its efferent, A its afferent side, and *f* the field of conjunction.

Fig 23



The ordinary reflex is produced by the stimulating electrodes being applied to an afferent nerve, the posterior root at B, and the effect recorded by contraction of the muscle M. If the distances BA and EM are known, and the latency delay in the muscle, then it follows that by subtracting these from the total time expended in the execution of the phenomenon we obtain a residue which is the actual delay of transmission of the excitatory effect within the centre EA itself

This we have done as follows —

#### SIMPLE Reflex Delay, two Experiments (Cat)

	Second
1 Total expenditure of time between excitation at B and contraction at M . . . . .	022
2 Time expended in transmission from B to A and E to M at 33 metres per second . . . . .	·006
3 Time expended in latency of muscle at M . . . . .	01

The sum of 2 and 3 gives all the time expended in extrinsic duties ; the subtraction, therefore, of these from 1, gives the delay or loss of time in the centre itself, this amounts to 006 (in one case ·004)

We now turn to what is more interesting, viz., the loss of time when the impulse

coming to the centre approaches it by way of the pyramidal tract which runs in the lateral column, and is marked as a thick interrupted line in the diagram and by the letters *py*

To obtain the time loss we have as before to take the total time expended from the moment of excitation at L to that of the contraction of the muscle M, and then to subtract from it the time occupied in simple transmission along the line LfM, and, finally, to subtract the latency time of the muscle. These times are as follows —

DELAY in the Spinal Centre during Excitation of the Lateral Column

	Average of four experiments (Cats)
	Second
1 Total expenditure of time from L to M .	0.176
2 Time expended in transmission from L to <i>f</i> , and E to M	0.06
3 Time expended in latency of muscle .	0.1

On subtracting 2 + 3 from 1, we get as a final result 0.016. This resultant loss of time is thus several thousandths of a second shorter than the delay taken by transmission of the reflex effect. This is naturally to be expected as a consequence of the lesser amount of centre to be traversed, but possibly the smaller result is also due to the channel of the pyramidal path in the nerve centre being “polarised” for descending and efferent impulses.

It appears, therefore, that when the impulses have to pass through the whole central structure (as in reflex) they suffer both a delay in time and a very marked reduction in quantity, and that when they pass through a portion which excludes the afferent commencement of the centre (cortical discharges), although the reduction is very considerable, the delay is much less.

There is one point to which it is necessary to draw attention before leaving this part of the subject, namely, the well-known susceptibility of central mechanisms to changes from fatigue, these altering the amount of nerve energy discharged. It will be sufficient here to indicate by two examples the influence which previous activity has upon the amount of nerve energy reflexly discharged from a spinal centre, the latter being indicated by the electrical effect in the issuing nerves.

## EFFECT of an Interval of Rest on the Simple Reflex Discharge

	Galvanometric deflections	
	Before rest	After rest of 15 minutes
Excitation of the central end of the left 7th lumbar posterior root gave in the left sciatic nerve	16	42
Excitation of 1st sacral as above	20	39

## EFFECT of Want of Rest on the Simple Reflex Discharge

Cat (263) Excitations following at two minutes' interval of right 7th lumbar posterior root gave in the right sciatic nerve	{	18	Coil 2000
		15	„ 4000
		After 15 min rest	
		12	„ 2000
Cat (378) Excitations following each other at 1 minute's interval	{	17	4000
		26	Coil 2000
		8	„ 4000
		31	„ 8000
		8	„ 8000

*Character of the Electromotive Change which is Produced by the Discharge of a Nerve Centre as Contrasted with that Artificially Induced in a Nerve Channel, i.e., Fibres.*

The galvanometric method appears to us to suggest differences between the passage of the nerve excitatory condition (so called "nerve impulses") along fibres according to whether it is a centre which is the source, or an artificial stimulus in the actual course of the fibres. Thus, if a peripheral nerve be excited directly by any form of excitation, i.e., electrical or mechanical, the effect in the nerve (i.e., the excitatory condition) shows itself in the galvanometer as a movement which begins sharply and proceeds moderately rapidly, but steadily, so long as the excitation lasts, stopping when the stimulus is left off; upon which return of the needle to zero begins.

It is quite otherwise when the effect in the nerve is due to the passage of the excitatory condition (the "discharge") from a nerve centre. When this latter is excited and the electrical change in the efferent path observed, it shows itself as a slowly developed deflection which gains speed as it moves, does not stop immediately when the stimulation is left off, and only slowly returns towards zero, which it frequently does not completely reach. This peculiar character of the deflection movement is special and easily recognised. If the activity of the centre be impaired, e.g., by cooling, drying, &c., the movement is still more sluggish, and is perhaps of more interest; it is *late* in development, i.e., does not commence for one or two seconds after the excitation has begun.



A similar increase of the normal latency in the discharge of the cord, we have also observed by the graphic method, and delay of the kind is frequently noticed in the cortex cerebri (FRANÇOIS FRANCK) when its activity is depressed by any of the agencies referred to on p 483

#### SECTION 4 — THE INFLUENCE EXERTED BY ITS CENTRAL ATTACHMENTS UPON THE ELECTRICAL CHANGES EVOKED IN A DIRECTLY EXCITED NERVE

We found, in the course of our experiments upon the nerve roots, that the amount of the electrical change in the nerve evoked by direct excitation of its fibres in any root, varied with the condition of the nerve centres, and was always less when the root was cut away from its central attachments

We, therefore, designed a series of experiments to test the extent of this influence in the case of the anterior and posterior roots respectively

This series of experiments consisted in the exposure of the cauda equina, after division of the spinal cord in the dorsal region, connecting the central end of the cut sciatic nerve with the galvanometer, and then raising the posterior roots *seriatim*, and exciting each with the platinum electrodes under all the precautions stated in Chapter III, Section 4 After measurement of the effect observed in the nerve to follow excitation of any posterior root in continuity with the spinal cord, the root was divided about its middle and the peripheral end gently ligatured, raised in the air and excited The resulting electrical change or effect in the nerve was noted and compared with that obtained from the root when first excited in continuity with the cord.

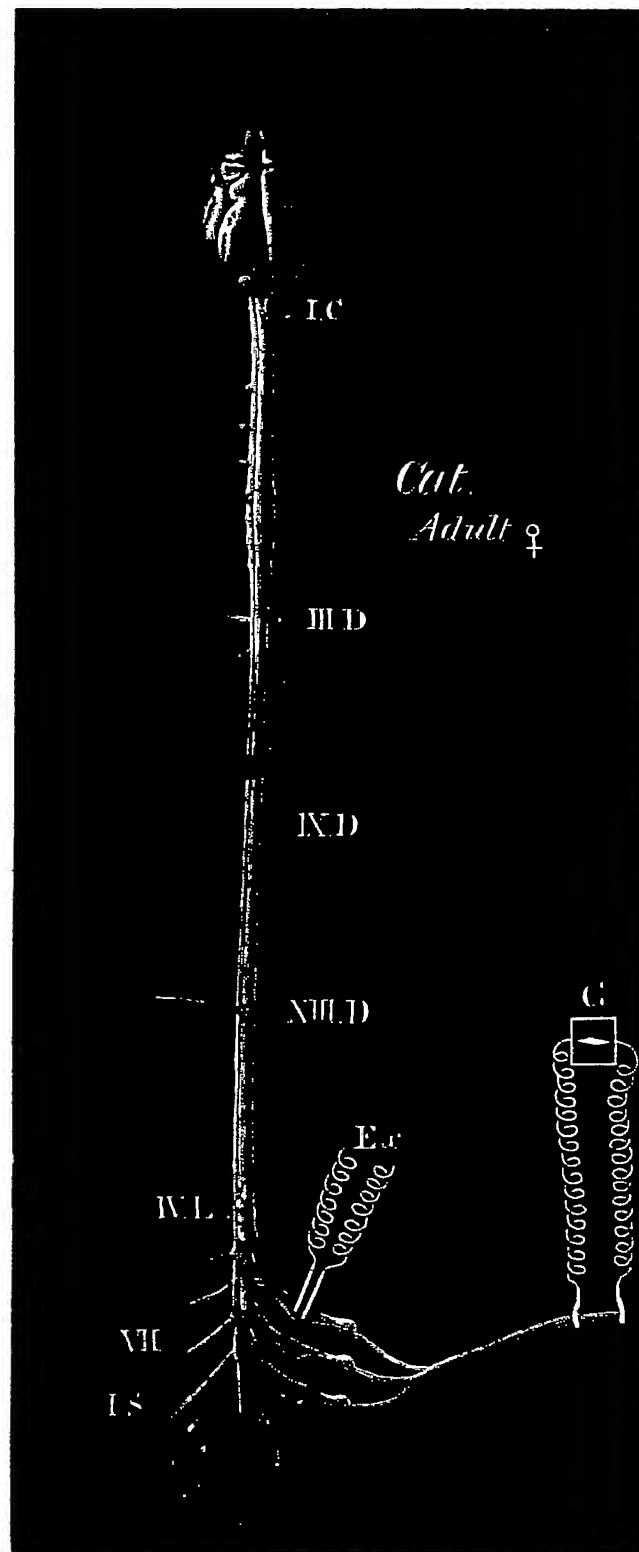
In every case a diminution was observed in the effect as a direct consequence of severing the peripheral portion from the central apparatus We feel justified in attributing this change to the cause assigned since the immediate local effect of the section on the peripheral fibres would be to raise rather than depress their excitability. The result, if marked, although conceivably due to the depressing effects of injury, is possibly associated with a loss of a beneficial (nutritive ?) influence derivable from the spinal centres The deflections observed were as follows —

#### AVERAGES

Posterior root excited	Effect in nerve	
	Root excited in continuity with cord	Root cut and peripheral end excited
6th lumbar . . . . .	267	227
7th lumbar . . . . .	259	172
1st sacral . . . . .	212	75

Averaging all the observations together, we find that the excitatory effect observed in the nerve, when the uncut root was excited, amounted to 237 scale, whereas that evoked by stimulating the peripheral end was 152 scale. The reduction amounts roughly to about 30 per cent of the original value, and is especially marked only in the

FIG 24



case of the posterior roots. This fact led us, at first, to believe that when a posterior root was excited in its continuity, the spinal centre being of necessity aroused, there must be a flow of energy from the latter down the root, and that this would provide the greater effect noted. This view, however, was materially shaken by the small amount of the reflex discharge obtainable from a nerve centre. We, therefore, regard

the phenomenon from the more general point of view expressed above until further research shall make the question clearer.

Meanwhile in this place we wish to add a few remarks on a curious result which we occasionally obtained (and the meaning of which is very doubtful) by varying the above-mentioned experimental procedure

As before, we connected the sciatic nerve with the galvanometer, and exposed the cauda equina after section of the cord in the dorsal region. Each posterior root was now excited in continuity with the cord, *separatim*. The anterior roots were then cut, and the excitation repeated.

In this preparation, therefore, we had the arrangement indicated in the diagram. (Fig 24) The first experiment of the kind was simple and uncomplicated, and may therefore serve as an example.

CAT (177). Sciatic Nerve and Roots of the Right Side prepared after Section of the Cord in the Dorsal Region.

Time	Excitation	Duration of same	Posterior root excited in continuity	Deflection, galv. scale	Reflex action as observed in muscles
12 26	4000	5 seconds	7th lumbar	70	Good reflex action
12 31	"	"	1st sacral	46	" " "
12 39	"	"	6th lumbar	62	" " "
12 45	Anterior roots of the above numbers divided				
12 50	4000	5 seconds	7th lumbar	380	Very vigorous reflex, much more than before
12 53	"	"	1st sacral	240	" " "
12 55	"	"	6th lumbar	280	" " "

It will thus be seen that section of the anterior roots seemed to enormously increase the effect in the nerve. We were quite at a loss to understand this result and therefore repeated the experiments. We then found that this striking difference was not always obtainable. In one experiment, for example, in which the section of each anterior root alternated with excitations of the corresponding posterior root, the rise of effect was only noted with one root—viz., the 7th lumbar—in which the effect mounted from 130 to 160, 147, 250, whereas the other roots showed no rise. In this experiment we noted that there was cooling of the preparation, especially of the lower roots. In a succeeding experiment (Cat, 182) we found that warming the cord had a very noteworthy effect on the result, whereas warming the root had not. We then made a fourth experiment (Cat, 268), in which the arrangement of the first was more closely adhered to

## CAT (268) Influence of Section of Anterior Roots on the Excitatory Effect in the Nerve, when one Posterior Root is excited in continuity

Time	Excitation	Duration	Root excited	Deflection
12 3	1000	3 5 seconds	7th lumbar posterior, in continuity	230 Average of two observations
12 6	2000	"	" "	275
12 10	Section of the anterior roots of the 5th, 6th, and 7th lumbar, and 1st and 2nd sacral			
12 20	1000	"	" "	245 Average of two observations
12 25	2000	"	" "	320
	Section of the 6th lumbar and 1st sacral posterior roots			
12 38	2000	"	" "	292
12 46	2000	"	" "	310

On summing up these experiments it is evident that the division of the anterior roots does raise the value of the effect in the sciatic nerve evoked by excitation of a posterior root in continuity. In the last three experiments that rise is not so greatly marked as to be more than the supplementary discharge of the spinal centres might account for, but this, of course, does not explain the high readings in the first case

## SECTION 5.—THE SPREAD OF REFLEX DISCHARGES UP AND DOWN THE CORD (INTERNUNCIAL FIBRES).

We have frequently spoken of the existence of internuncial fibres connecting the various centres. It must, however, be confessed that the evidence of their existence is founded almost entirely upon our knowledge of the laws of reflex spread as stated by PFLUGER (See Section 1, p 484)

We endeavoured to ascertain what light the present galvanometric method would throw upon this spread, and thus upon the localisation and characteristics of these paths. To elucidate this we made a series of experiments in which the cord was excited and the electrical changes noted at the same time that the muscular movements were either recorded or carefully observed

(1.) *Ascending Discharges (Reflex).*

In the case of reflex discharges it is possible, after division of the cord, to observe the electrical changes in the upper end of the lower fragment of cord, and at the same time to note the contractions of a muscle of the lower (hind) limb

Since it was desirable to ascertain the relationship between the periodicity of the electrical changes in the cord and that of the muscular twitches, the capillary electrometer was used.

The spinal cord of the Cat being divided in the mid-dorsal region, the upper end of the dorso-lumbar portion was prepared for connection with the electrometer, whilst the lower tendon of the rectus femoris muscle was cut and attached to one of FICK's spring recording levers (isometric method). The cord was then exposed over the dorso-lumbar junction and the lateral column excited with stimuli of varying degrees of intensity. It is obvious that electrical changes thus produced in the cord are due (a) to the excitation of continuous fibres joining the excited portion of the lateral column with the observed region, (b) to the excitation of indirect fibres in the lateral column, internuncial or otherwise, (c) to the discharge of nerve impulses up the cord from the aroused centres.

The main interest of the experiment lies in the fact that with a weak stimulus no muscular effects were observed, although distinct electrical effects were produced, whilst with a strong stimulus the centres in the cord were so aroused that they continued to discharge after the stimulus had ceased, these discharges being evidenced both by muscular contractions and by effects in the electrometer.

The following Table indicates this result —

EXPERIMENT. Cat (104).—Afferent Effect in Cord compared with Contraction of the Muscle, simultaneously evoked by Intermediate Excitation of the Cord

Time	Excitation	Duration of same	Effect in cord, electrometer	Effect in muscle, spring myograph
4 50	1500	5 secs	Persistent 2 divs	Nil
4 54	3000	"	" 6 divs	Twitch
4 55	4000	"	" 7 divs	Initial effect and continued tetanus
4 57	5000	"	" 11 divs, followed by intermittent after-effects	Initial characteristic (cord) contraction followed by well-marked after-effect

It is thus seen that when a lumbar spinal centre is aroused to discharge, a flow of nerve energy takes place up the cord as well as out by the efferent roots, and, in all probability, impulses thus pass upwards to various groups of centres both in the upper regions of the cord and in the encephalon.

As to the spinal channels by which these impulses travel,—whether internuncial, direct efferent fibres (pyramidal tract) or direct afferent fibres (posterior column)—the experiment gives no information, and we have not had an opportunity of repeating it on an animal in which, by previous operations, the two latter have been more or less eliminated. Some evidence is afforded by the following experiment, in which the left

posterior column having been divided at the 9th dorsal vertebra, the left 1st lumbar posterior root was excited, and the electrical changes in the cord noted galvanometrically at the same time that the muscular movements were observed

It will be seen that the electrical change in the dorsal region of the cord was indicated by an effect of 55 in the galvanometer, when the lateral column on the side of the excitation was uninjured, whereas hemisection between the root and the observed region cut down the galvanometric effect to only 7. Before the interruption by the hemisection, a reflex contraction was observed during the excitation in all the muscles supplied by the various nerve segments between the excited root and the observed area of cord, whilst, after the section, such reflex contraction was limited to the piece of cord below the hemisection. The particulars of this second experiment, which appear to suggest that the internuncial fibres are localised in the lateral column, are as follows —

Cat 376. Cord divided, and peripheral end connected to the galvanometer at the intervertebral disc between the 8th and 9th dorsal vertebræ, section of the *left* posterior column opposite 13th dorsal vertebra

Time	Excitation	Duration of excitation	Part excited	Effect in galvanometer	Effect in neighbouring muscles
6 3	8000 (Strong stimulus)	5 secs	Left 1st lumbar posterior root	55	Powerful reflex in trunk muscles

Left hemisection of the cord was then performed at disc between 13th dorsal and 1st lumbar vertebræ.

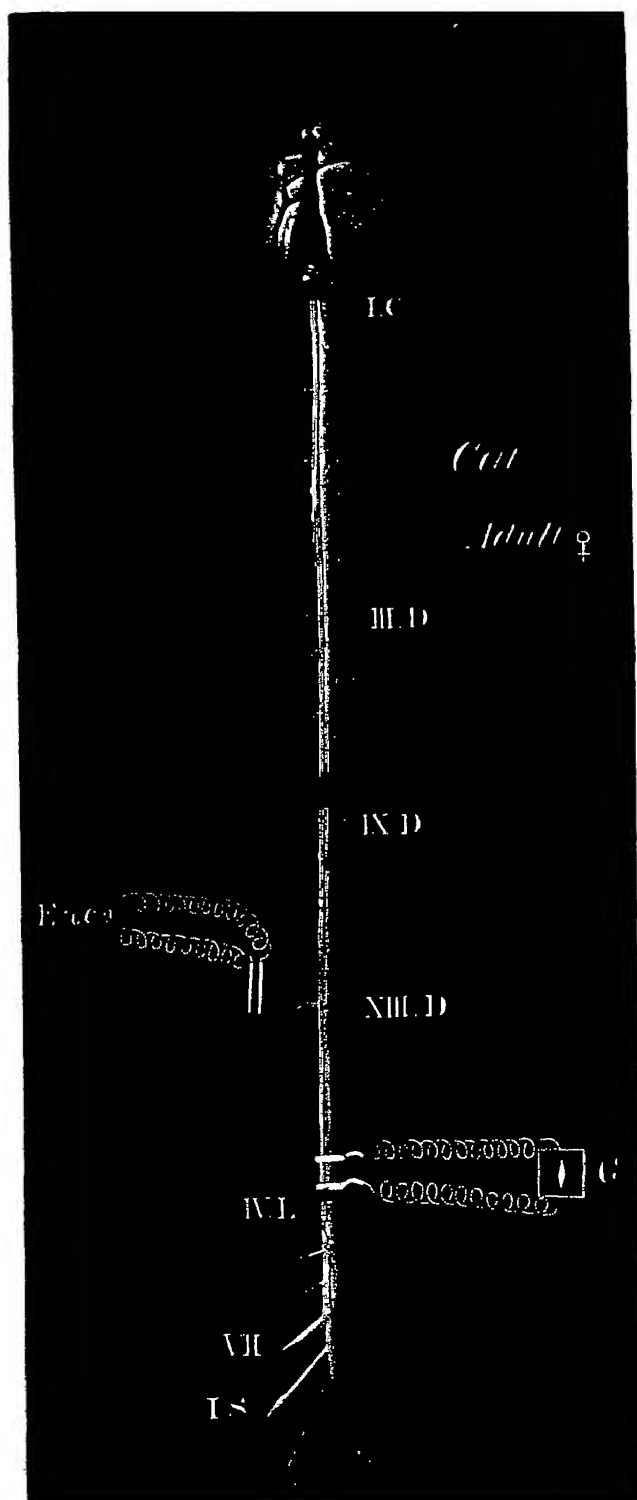
Time	Excitation	Duration of excitation	Part excited	Effect in galvanometer	Effect in neighbouring muscles
6 12	8000	5 secs	Left 1st lumbar posterior root	7	Reflex limited to muscles below the point of hemisection

## (2) *Descending Discharges*

While PFLUGER's law concerning the upward internuncial discharge of spinal nerve centres undoubtedly prevails, nevertheless the anatomical investigations of LOCKHART CLARKE, the physiological observations of BROWN-SÉQUARD, and the anatomical researches of GOLGI, recently confirmed by RAMON Y CAJAL, show that there must

be descending channels from at least the afferent sides of the spinal nerve centres, even if there are not direct descending channels. In fact, GOLGI's work goes to show that there are such direct paths, and this is extended by KOLLIKER. We commenced the investigation of this point by the galvanometric method with an attempt to

Fig 25.



ascertain whether any electrical change can be detected in the cord below the entry of the stimulated afferent nerve, and have obtained positive results. Our plan was to divide the cord in two places, as in Chapter VIII., and to connect the lower lumbar end of the tract included between the sections with the galvanometer. (See fig. 25.)



The trunk of the last dorsal nerve was then excited

Cat 378. Cord divided between 8th and 9th dorsal vertebræ, and at disc between 3rd and 4th lumbar vertebræ.

Excitation of left 13th dorsal nerve, effect in lower (lumbar) portion of cord

Time of observation	Intensity of stimulus	Duration of stimulus	Effect in galvanometer	Effect in muscles
11 33	2000	seconds. 5	26	Fair reflex
11 36	8000	5	31	Fair reflex

In order to see whether this effect was transmitted by the fibres in the posterior or lateral column, the left posterior column was now divided opposite the centre of the body of the 1st lumbar vertebra. The excitation of the root now gave the following effect —

Time of observation	Intensity of stimulus	Duration of stimulus		Effect in galvanometer	Effect in muscles
11 58	8000	seconds 5	Left 13th dorsal nerve, central end	8	Good reflex
12 4	Left lateral column divided (hence complete left hemisection)				
12 15	8000	5	Left 13th dorsal nerve, central end	6	

We here see most unmistakably that the descending effect is very different in character and localisation from the ascending effect previously described, for (1) it is much smaller, (2) it is mainly dependent upon the continuity of the *posterior* column, whereas the ascending *indirect* effect is dependent upon the integrity of the lateral column.

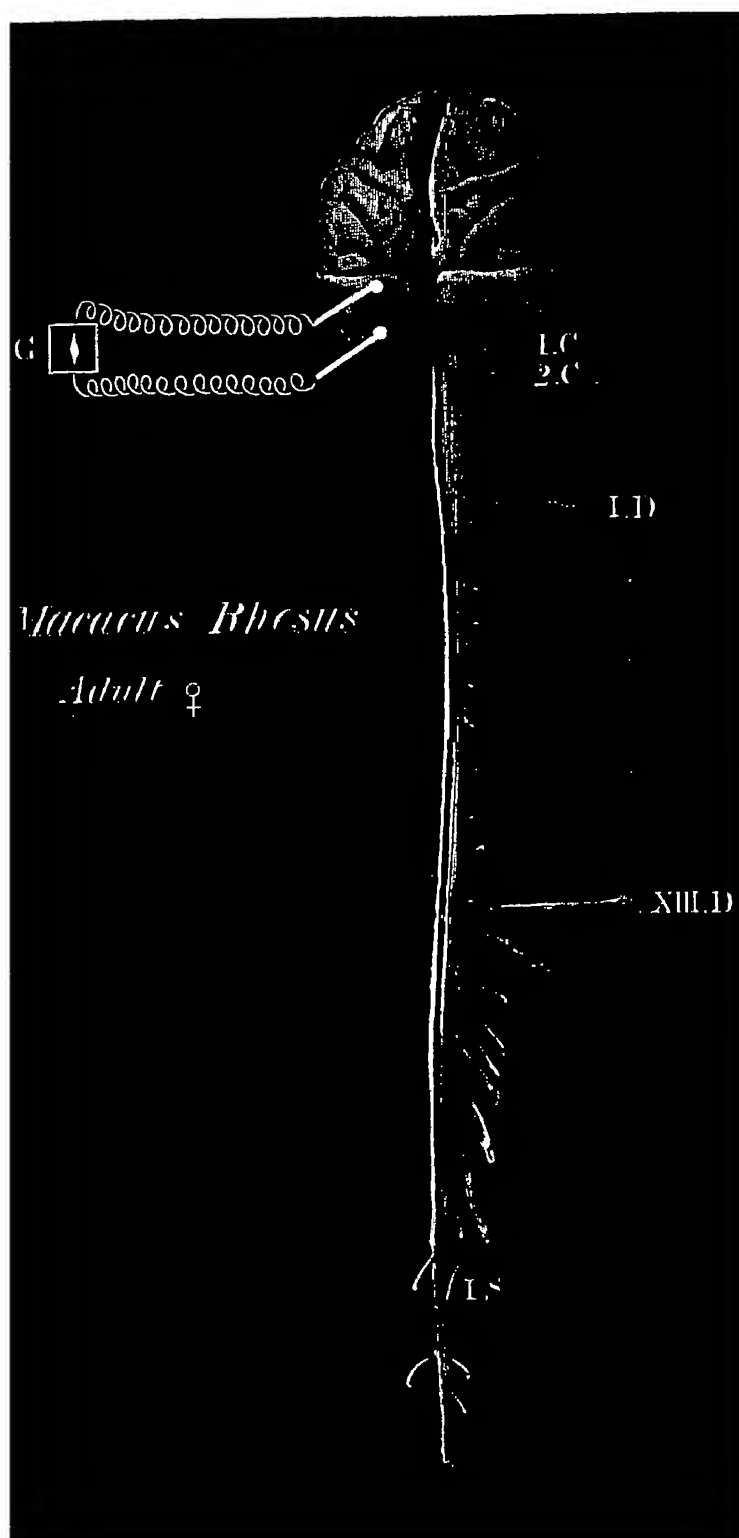
These results, which were quite unexpected by us, are in very remarkable agreement with the anatomical researches of GOLGI, &c.

#### SECTION 6.—ON THE ELECTRICAL CHANGES IN THE CORTICAL NERVE CENTRES.

In all the preceding investigations we have studied the characteristics of a nerve centre by examining the electrical changes, and thus the excitatory processes present in the nerve fibres connected with such a centre. We chose the spinal cord since it contains the simplest form of a complete centre that the Mammalian nervous system presents

In an early stage of our work the possibility occurred to us of investigating the centres in the cerebral cortex, by the use of the electrical method, this plan having been previously employed by CATON (1875) We selected the occipital lobes (see fig 26), and endeavoured by stimulation of the retina to obtain evidences of definite

Fig 26



electrical changes in the cortex of the moderately etherised Cat, consequent upon the arrival therein of nerve impulses. The difficulties of effectual isolation and the uncertainties of the area of connection, comprising as it does a mass of subjacent nerve fibres, seemed to us to account for the indefinite and capricious character of the electrical indications as displayed by the galvanometer

The experiments of BECK, of FLEISCHL VON MARXOW, and of DANILEWSKY in this connection have been referred to in Chapter II, which deals with the history of the electrical method. With reference to these we would here only point out that the experiments of SETSCHENOW, WERIHO, and ourselves, to which in his Polish paper BECK alludes, seem to us to indicate that the *observed* electrical changes may have their seat in nerve fibres proceeding from or to centres, rather than in any form of central, *i.e.*, corpuscular, nerve mechanism.

Any electrical changes in the contacts of the electrodes with the cortex might, therefore, be as much caused by the impulses travelling in the subjacent fibres as by changes in the cells or other surface termini.

The above criticism obviously does not affect the evidence which the presence of definite electrical changes offers as to localisation, but seems to us to discount any advantage which the method might offer for the investigation of the functions of a nerve centre by the study of the actual changes in its cells.

### SUMMARY

It is obviously impossible to formulate with sufficient accuracy many general conclusions as to the mode in which the functional activity of the spinal nerve centres is generated and discharged, but we cannot refrain from pointing out that the electrical method supplies many ways of investigating this very important and difficult subject, and further that it throws most unexpected light on the obscure questions relating to the working of the several parts of nerve centres.

Most prominently stand out two principal facts —

- (1) The kinetogenetic portion\* of a spinal nerve centre is probably the afferent side. (See Section 2.)
- (2) The part in which the delay and diminution of impulses passing through is effected is the efferent side of such a centre with the field of conjunction. (See Section 2.)

The consideration of these facts, unexpected as they were, shows clearly that the interpretation by BASTIAN† of sensori-motor nerve phenomena is probably the most correct yet advanced. The basis of that interpretation, namely, the doctrine of kinæsthesia as formulated by him, is in complete harmony with our experimental results.

BASTIAN has for many years contended that the ordinary division of nerve centres or parts of the same into *sensory* and *motor* respectively is misleading, and that not only has the statement that the source of a nerve centre's discharge is the *motor* part

\* By the term "kinetogenetic portion" we have styled that part of a centre in which the potential energy is converted into kinetic.

† "The Brain as an Organ of Mind" "Paralysis, Cerebral, Bulbar, and Spinal"

of it no basis of actual fact, but that it is more philosophical to associate such source with the sensory part.

Among the considerations which favour this view are the following —The undoubted physiological resemblance which exists between the succession of events in a voluntary or reflex movement, respectively, and the analysis of such psychological events as are known to be concomitants of the former. The psychological phenomena of reflex action show that the afferent impulse in all cases precedes the efferent discharge, psychological analysis also shows that muscular sense impressions similarly precede those discharges which evoke "voluntary" coordinated movements. Hence he concluded that since the sensory excitation always precedes the efferent output, the former must have primary importance, in other words, that the development of kinetic energy must take place in the afferent side of the centre. To express this view briefly he coined the term *kinæsthesis*.

As the electrical method affords the first opportunity of an experimental contribution to this subject, it is interesting to find how strongly its application bears out BASTIAN'S position. In this chapter it appears probable that the kinetogenetic portion of the centre is the afferent side of it, and the more especially when it is seen how readily the centre discharges into the afferent nerve channels (*i.e.*, actually "backwards," as compared to the course of ordinary afferent impression).

The method has further enabled us to ascertain what connections and facilities for conduction the efferent, or so-called motor side of a nerve centre possesses, and instead of finding, as might have been expected from the ordinarily expressed beliefs on this subject, that we had to deal with a source of energy that was readily aroused, and freely connected with its neighbours, we found, to our surprise, that it afforded nothing of the sort, and that its power of conducting impulses centripetally was apparently *nil*.

Curiously enough, this last point was foreseen also by JAMES, who, in his celebrated work on the 'Feeling of Effort,' 1880, while endorsing the views of BASTIAN, says that the "electrodes of the physiologist," if applied to the central end of the anterior root, would not arouse any "sentient," *i.e.*, afferent impulse in the cord. We are happy to find that our experimental results, unusual though they were, are, nevertheless, in close agreement with the deductions of the logical method of these distinguished writers.

## CHAPTER XII—ON THE ELECTRICAL CHANGES EVOKED IN THE SPINAL CORD AND NERVES BY THE ACTION OF ABSINTHE AND STRYCHNIA

## SECTION 1.—EXPERIMENTS (CONTROL) INCLUDING THE USE OF ABSINTHE

Very early in the present investigation on the effects produced by electrical excitation of central apparatuses, the advisability of obtaining a control of our results presented itself. The use of strychnia by DU BOIS-REYMOND as a control demonstration of the excitatory electrical state in nerves, formed, as it always must, the basis of such a method.

We, however, first selected absinthe as particularly exciting nerve centres, and, according to one of us\* (V H), specially the cortex. Absinthe has been known since the experiments on animals by MARCÉ† to cause, in small doses, effects only explicable as poisoning of the highest cerebral centres, thus producing mental changes, delirium, hebetude, &c, while in larger doses it evokes clonic epileptiform convulsions with stertorous respiration, &c.

MAGNAN‡ has, of all writers, contributed the most to our knowledge of the action of this substance.

By injecting small quantities of the essence of absinthe either into the stomach or into a vein, he produced a very striking series of phenomena, which he showed were identical with idiopathic epilepsy.

Following up its action more closely he endeavoured to ascertain the share taken in the production of the fits by the brain and spinal cord respectively. This he investigated by first dividing the cord at the atlanto-occipital articulation, and then injecting absinthe, artificial respiration being kept up.

Unfortunately, he only describes one experiment (No. 6) in which the cord was completely divided. He concludes, however, from his other experiments that the drug excites simultaneously the lower (spinal) and the upper (cerebral) centres. It has, however, been shown by one of us§ that complete section of the cord at the 8th dorsal vertebra prevents the appearance of the characteristic convulsions in the muscles of the parts below the level of the section; and, further, that the corresponding parts or limbs, if the excitable cortex of one side be removed, will not take part in the first general epileptiform convulsions which follow the injection of the drug, whilst, even when in the subsequent fits such parts are affected, the muscles only pass into a slight degree of tonus.

Until a more extended series of researches should negative these points, it is

\* 'Brown Lectures'

† 'Comptes Rendus de l'Académie des Sciences,' vol. 58, 1864, p. 628; also AMORY.

‡ 'Recherches sur les Centres Nerveux,' Paris, MANON, 1876.

§ 'Reports of the Brown Institution'

reasonable to accept the conclusion that absinthe excites *par excellence* the complex cortical centres.

It will be well, perhaps, to mention that by the method of simple observation the following phenomena are elicited by the excitatory action of absinthe

After injection of two drops of essence of absinthe\* into the jugular vein of an animal, narcotised with ether to the degree of unconsciousness, there occur, after a sufficient interval has elapsed (30 seconds or so) to permit of the translation of the poison through the heart and lungs to the arterial system, and so to the brain, the following events —

The small facial muscles begin to twitch in single clonic spasms, next passing into a state of tremulous tonic spasm. This order of convulsion passes rapidly down the body, until the tonic spasm in the limbs is extremely marked. After this has obtained for a period varying with the dose injected, the tonic spasm gives way to a long series of clonic twitches. Accompanying these motor “discharges,” there is profuse salivation, and sometimes escape of urine, while in cases in which narcosis has not been preliminarily employed, unconsciousness and coma are early symptoms.

It is thus obvious that absinthe affords a very simple and efficient means of chemical excitation for the purpose of testing the validity of the results of electrical stimulation of the motor cortex.

We have employed it under the following experimental conditions —

- (1.) Connecting the nerve to the galvanometer or electrometer.
- (2.) Connecting the spinal cord to the galvanometer or electrometer, at the same time observing the contractions of the muscles in different parts.

The method employed was, so far as the electrical connections of the observed parts were concerned, precisely that described in the preceding pages. Special precautions had to be taken against any agitation of the preparation. The narcosis with ether being temporarily maintained, the external jugular vein of either side was exposed, penetrated by the needle of a hypodermic syringe, and two minims of the essence of absinthe injected, the narcosis of this drug taking the place of the etherisation, which was forthwith terminated. It was invariably observed that the galvanometer showed evidences of excitatory electrical changes in either nerve or cord, before the muscular contractions in the immediate neighbourhood of the observed level became accentuated.

In respect of what has been said above, we may here add that we never saw contractions of muscles innervated from points below the level of section in the spinal cord when that was divided.

\* Obtainable of Messrs HOPKIN and WILLIAMS

(1) *Excitation of the Intact Central Nervous System by Absinthe —Electrical Effects in the Sciatic Nerve*

The results obtained by this arrangement were as follows :—

(a) *Observations with the Galvanometer* —The experiments were made on four Cats, one to fifteen drops of absinthe being injected. The preliminary effects noted in the galvanometer while as yet the spasms were limited to the upper anterior muscles of the body amounted to small deflections, of which the following are examples 4, 5, 5, 8, 10, 10, 13, 15

When, however, the toxic effect of the drug became more marked, and the discharges summated produced a fully developed fit, as above described, then the deflection of the galvanometer was notably increased, and ran up to maxima of 135, 150, 150, 185, 210, 272, 275, these averaging nearly 200. In smaller attacks, but still generalised, the deflection varied from 45 to 85. With regard to the magnitude of these deflections, it is to be noted that their large amounts are doubtless due to the completely bilateral and prolonged character of the cortical discharges and the continued effect on the galvanometer.

(b.) *Observations with the Electrometer* —When during any one of the above observations the electrodes in contact with the central end of the nerve were switched over so as to bring it into connection with the electrometer, the effect was visible, but varied notably in amount from a small movement of the mercurial meniscus to 1 division.

It was thus abundantly clear that the employment of absinthe gave maximal electromotive effects in the sciatic nerve through the overwhelming discharge of the highest cortical centres, and the figures obtained from the galvanometric deflections give a fair notion of the comparative magnitude of these discharges, the more especially as the degree to which the epileptic discharge developed could be plainly seen in the amount and duration of the spasm in the neighbouring muscles. This being so, it is, of course, hardly necessary to add that the cessation of the convulsion was synchronous with a halt in the swing of the galvanometer needle.

(2) *Excitation of the Nervous System by Absinthe —Electrical Changes in the Spinal Cord*

As might have been anticipated, the electrical effects observed in the spinal cord when the central mechanisms were excited by a diffuse stimulus, such as that of absinthe in the circulation, were larger than that witnessed in the peripheral nerve.

We have made four experiments in Cats, and one in the Monkey (*Macacus rhesus*), and have usually measured the effect with the electrometer. With this instrument the excursions of the mercury were very marked, varying from slight movement in the case of initial spasms to excursions of even five divisions in severe fits.



In the galvanometer, similarly, the lowest recorded deflection was 110, the highest being over 300 and obviously conditioned by the duration of the convulsions

No comparison can be drawn between the magnitude of the deflections and those obtained from the nerve, for the above and other reasons. In general they confirm the validity of the views advanced, respecting the results obtained by electrical excitation of the central nervous system as detailed in the foregoing chapters

An experiment in this connection may here be mentioned as of special interest regarding the action of absinthe. The toxic action of this drug is unquestionably excitatory as far as the highest nerve centres are concerned. FRANÇOIS FRANCK\* found that it produced inexcitability of the cortex. One of us has previously suggested that this is a question of dosage, in common with other narcotic agencies. In the present series, while observing in one case the deflection produced by absinthe, we superadded electrical excitation of the previously exposed cortex. The result (Cat 99) was to notably increase the effect. Thus, while the chemical stimulus was actually evoking a powerful discharge, the additional electrical excitation caused the centres to produce still more kinetic energy. In this stage, therefore, the absinthe had not exhausted the cortex. The additional effect was visible, both in the electrometer and galvanometer, when either was switched on to the cord

## SECTION 2.—EXPERIMENTS (CONTROL) INCLUDING THE USE OF STRYCHNIA.

The method of employing strychnia differed from that detailed in the case of absinthe in one important particular, namely, that the spinal cord was severed from its connection with the encephalon. The spinal cord in two Cats and one Monkey, and the sciatic nerves and the posterior root in two Cats, were connected with the galvanometer for observation of the excitatory electrical changes. The solution of strychnia employed was a 1 per cent solution of the acetate. It was injected into the peritoneal cavity, and the toxic symptoms observed. The tetanic spasms, like those obtained by absinthe, were of very varying force and duration, but gave far higher readings than absinthe. We will return to this point later, and meanwhile briefly state the results obtained

(1) *Electrical Effects in the Sciatic Nerves.*—The observation of the effects in the Mammalian nerve during the discharges due to strychnia has furnished valuable control results. We have, however, used the method to obtain by its means the evidence referred to in the preceding chapter on the discharge of a nerve centre backwards down the posterior root as well as the discharge down the anterior roots.

(2.) *Electrical Effects in Posterior Root.*—Similar changes to those in the nerve have been obtained in the case of the posterior root. These have been already referred to in Chapter XI., Section 3.

(3) *Electrical Effects in the Spinal Cord.*—When the spinal cord of an animal was

\* *Loc cit*

severed, and the lower fragment connected in the manner practised in all the preceding experiments, and strychnia injected, very large electrical changes were observed. These were produced in the upper, as well as the lower, end of the dorso-lumbar portion of the cord. The maximal effects were over 500 scale of galvanometer, and the average in one experiment of all the readings was as high as 300.

To sum up these experiments with a chemical stimulus, from the point of view from which they were designed, it is clear that the excitatory electromotive changes (*i.e.*, diminution in the resting difference) observed to occur in the central nervous system when that is excited electrically or mechanically, are true indications of physiological phenomena accompanying functional activity, and, further, that their amounts vary directly in proportion with the intensity and duration of such activity.

### CHAPTER XIII — SUMMARY AND CONCLUSIONS

The consideration of the results given in the foregoing chapters shows, we venture to think, that the electrical method of investigating the localisation of nerve impulses in the Mammalian nervous system is one which has furnished several new aspects of nerve function, and we believe that if further pursued it will prove one of the most valuable means of differentiating the structure of the nervous system, and gauging the nature of the functional activity of the nerve centres.

In view of the extended scope of our present research, we feel unable to give a sufficiently brief summary of the results. We therefore propose to enumerate, by way of conclusion, some of the general principles which we think we are justified in deducing from our work.

The following remarks, therefore, cannot in any sense be regarded as embodying the whole of our investigations, and we must consequently refer our readers to the individual chapters, and especially to the remarks at the end of each, for information as to points upon which we do not here touch.

#### (1) *Resting Electrical Difference.*

The resting electrical difference between the cut and uninjured longitudinal surface respectively in the Mammalian mixed nerve, spinal nerve root, and spinal nerve, has been found by us to have the following value —

	Cat	Monkey.
Nerve	(69 cases) 01 Daniell	(12 cases) 005 Daniell
Root	(5 cases) .025 „	
Cord	(50 cases) .032 „	(10 cases) .022 „

We have found, further, that the difference is subject to variations of which the following are the most important —

(a) A notable fall is observed in all three tissues in consequence of systemic death

(b.) The difference in the cord is increased after the functional activity of the organ has been aroused

(c) The difference in the cord is more pronounced when the tissue is in connection with the encephalon (See Chapter IV.)

## (2) *Effect in the Spinal Cord on Excitation of the Cortex Cerebri*

In extension of our discovery that excitatory electrical effects can be observed in the spinal cord to result from excitation of the cortex cerebri, as previously described, and by means of which the character of the impulses derived from the cortical centres may be studied, we have obtained effects in both the cord and the mixed nerve, following similar excitation of the cortex, and by comparing the result of these observations together have found that the excitatory state evoked by cortical activity undergoes a diminution of over 80 per cent. in the passage from the cord into the sciatic nerve

We have also applied the galvanometric method to differentiate the cortical excitable areas, by recording and comparing the discharges from the same in the spinal cord, and have found a striking degree of localisation demonstrated thereby in the Cat as well as the Monkey. (See Chapter V)

## (3.) *Effect in the Spinal Cord on Excitation of the Corona Radiata.*

By a comparison made between the amounts of the electrical effects produced in the spinal cord and the mixed nerve respectively after excitation of the corona radiata, we found that the cord effect is four times as great as that in the nerve, and further, that this corona-radiata-to-cord effect is little more than half the complete cortex-to-cord change. (See Chapter VI)

## (4.) *Bilaterality.*

By comparing the records of the extent of the electrical effects in each half of the longitudinally divided cord, and in the mixed nerve of each side, we have made fresh observations on the important and complex question of bilaterality of representation in the central nervous system We have found—

(a.) That it is possible to obtain strictly unilateral effects in both the spinal cord and sciatic nerve with complete excitation of both cortex cerebri and corona radiata

(b.) That the circumstances which favour the production of bilateral effects are such as bring into play other portions of the central nervous system, *e.g.*, the opposite excitable cortex, cerebellum, and basal structures; and,

(c) That such bilateral effects, under these circumstances, can be evoked more readily by excitation of the corona radiata than of the cortex

Hence, we conclude that, as far as the cortical efferent representation of the lower limb in the Cat and Monkey is concerned, the normal condition is that of unilaterality (See Chapter VII)

(5.) *Electrical Changes evoked in the Spinal Cord by Excitation of its Columns.*

Observation of the electrical changes in the dorso-lumbar spinal cord, when evoked by direct excitation of its fibres after severance from the encephalon, has revealed by comparison of the electrical changes produced the proportionate existence of direct and indirect channels in the various columns of the cord.

We have thus examined the columns so far as they conduct ascending and descending impulses respectively in the Cat and Monkey. This analysis we extended by employing the exclusion method of intervening sections, as an addition to observations on the intact cord. The results show that —

( $\alpha$ ) In the Monkey a relatively larger number of direct fibres are contained in the lateral column than in the posterior column, the reverse being the case in the Cat.

( $\beta$ ) For both classes of impulses and of animals observed we have obtained ( $\alpha$ ) no evidence of crossing between the lateral columns, ( $\beta$ ) evidence of indirect connections between one posterior column and the lateral column of the same side, ( $\gamma$ ) evidence of cross connections between the posterior columns.

(c.) There is no evidence of the existence in the anterior columns of the cord (Cat and Monkey) of any continuous fibres between the mid-dorsal and lumbar regions.

(d) The spread of impulses from path to path in the spinal cord appears, in addition to what is stated under ( $\beta$ ), to be conditioned as follows.—The posterior column fibres spread into other columns more as they ascend than as they descend, whereas the fibres of the lateral column spread in a converse manner (See Chapter VIII)

(6) *The Relations of the Spinal Cord to the Lumbar Nerves.*

We have investigated the relation of the peripheral nerves and their roots to the paths and to the bulbo-spinal centres in the dorso-lumbar region of the spinal cord.

The investigations consisted in observing (A) the electrical changes produced by exciting the mixed nerves or their roots in the spinal cord when separated from the encephalon, (B) the electrical changes produced by excitation of the divided cord in the spinal nerves, and (C) the excitatory changes produced by stimulation of the spinal centres

A. The results obtained by the first method may be grouped as follows.—

( $\alpha$ ) By far the majority of afferent impulses ascend the cord on the same side as

the entering root, both by direct and indirect paths, a small minority ascend by the posterior column of the opposite side, and a mere fraction by the lateral column of the opposite side

(b) The direct path of afferent impulses is localised in the posterior column of the same side as that of the nerve or root excited.

(c) The indirect paths of afferent impulses are localised in the posterior columns of both sides, and in the lateral column of the same side as that of the excited nerve.

(d) The proportionate development of both systems of nerve paths in the two sides of the cord may be inferred from the percentages of the total transmission of excitatory electrical changes from the afferent nerve to the cord.

Of the electrical changes there are transmitted by —

					Same side	
Posterior column of same side as excited nerve	.	60	per cent	}	80 per cent.	
Lateral       ,,       ,,       ,,       ,,		20	,,			
					Opposite side	
Posterior column of opposite side to       ,,		15	,	}	20 per cent.	
Lateral       ,,       ,,       ,,       ,,		5	,,			
(See Chapter IX.)						

B The descending electrical effects, as far as the relationship of the cord and nerves is concerned, were investigated in the mixed nerve, the spinal cord being severed from the encephalon and excited.

The results of these experiments, obtained with both minimal and maximal stimuli, and controlled by the exclusion method of intervening sections, were as follows :—

(a.) On minimal excitation of the posterior column, impulses are directly transmitted into the posterior roots of the same side, and so into the mixed nerve; with maximal excitation some impulses are similarly transmitted through indirect paths

(b.) On maximal excitation of the posterior column, impulses are transmitted by indirect paths across to the posterior roots of the opposite side, and so to the mixed nerve of that side.

(c.) On excitation of the lateral column, impulses are indirectly transmitted to the mixed nerve of the same side as that of the excited column

(d.) The proportionate percentage of the total transmission of excitatory electrical states from the various excited columns of the dorsal cord into the mixed nerves is as follows :—

					per cent.		per cent
Excitation of posterior column of same side as observed nerve					73	} Same side	82
,, lateral       ,,       ,,       ,,					9		
posterior       ,,       opposite       ,,					15	}       ,,	18
lateral       ,,       ,,       ,,					3		

(e) Our evidence shows that electrical states (*i.e.*, impulses) are transmitted with great facility from the excited areas in the cord down the afferent channels of the cord, posterior roots, and nerves (see Chapter X)

C The researches into the relationship between the spinal cord in the dorso-lumbar region and the mixed nerve and spinal nerve roots, have enabled us to formulate some generalisations on the functional activity of the spinal nerve centres as follows —

(a) There is complete obstruction to all centripetal impulses which may reach the cord by the central end of the anterior root.

(b) A marked quantitative diminution as well as delay in time is suffered by impulses which leave the spinal cord by the anterior roots, whether these have originated in the cortex cerebri, corona radiata, or the lateral columns of the cord

(c) An increased resistance to descending, as compared to ascending, impulses by certain indirect paths is offered connected with the afferent side of the spinal centres

(d) Whenever a spinal centre discharges, nerve impulses pass from it down the posterior roots as well as the anterior

(e) The effect produced in a mixed nerve by the reflex discharge of a spinal centre down the nerve fibres is notably small when compared with that evoked by their direct excitation (see Chapter XI.).

It will be gathered from the extent and variety of the above conclusions that the employment of the method used in the above research has led us on from one investigation to another. We commenced our experiments with the object of ascertaining the character of the cortical discharge, and we employed for this purpose the capillary electrometer.

We then made use of the galvanometer for the same purpose, and at once found that a method was opened up for investigating, not merely the general characters of a cortical discharge of impulses, but the comparative amounts of such impulses when generated in different parts of the Mammalian nervous system. This led to its employment as a means of ascertaining the distribution of the channels in the spinal cord along which these impulses passed, and thus to the determination of the extent to which afferent as well as efferent nerve impulses were localised in fibres on one or the other side of the cord. The necessity of stimulating for this purpose the various roots of the nerves brought before us in a most striking manner the remarkable difference between the central connections of the two kinds of roots, and thus finally opened up the possibility of new investigations into the anatomical relations of a centre and the particular physiological attributes which characterise it

The correctness of the method is, we think, shown by the way in which the results set forth in the foregoing chapters were progressively obtained by its use. Many of them were unexpected by us, and needed ample verification. We had thus an opportunity, in frequent repetition of the same experiment, of probing the extent to which the data our method furnished could be relied upon. From this point of

view we are firmly convinced that, when proper precautions are used to avoid the disturbing influence of capricious factors, the present plan is one which gives as sure indications as any other method which has been used in the carrying out of investigations into the central nervous system, whilst by its mode of application it has the merit of ensuring definite localisation in hitherto unexplored regions. The wide extent of the field of research which the use of the method opens up is obvious. We have only employed it for elucidating a few of the phenomena which are exhibited by the functions of the brain and spinal cord, but the functions of various ganglia, the relations of the sympathetic system, of the more central portions of the bulbo-spinal system, and finally of the encephalic structures may, and undoubtedly will, be satisfactorily approached in the future by its means.



# APPENDIX A —Topographical Relations existing between the Superficial Origins from the Spinal Cord of the Spinal Nerves, and the Bodies of the Vertebrae in the Cat

CERVICAL NERVE	CORRESPONDING VERTEBRÆ
I	Upper border of 1st cervical
II.	Upper half of 2nd cervical
III	Middle of 3rd cervical*
IV	Upper border of 4th cervical*
V	Intervertebral disc between 4th and 5th cervical
VI	Lower border of 5th cervical and disc between 5th and 6th cervical
VII	Lower half of 6th cervical
VIII	Centre of 7th cervical
DORSAL	
I	Disc between 7th cervical and 1st dorsal
II	Lower border of 1st dorsal and disc between 1st and 2nd dorsal
III	Lower half of 2nd dorsal
IV	Lower half of 3rd dorsal
V	Lower two-thirds of 4th dorsal
VI.	Centre of body of 5th dorsal
VII	Lower half of 6th dorsal, and disc between 6th and 7th dorsal
VIII.	Lower half of 7th dorsal, and disc between 7th and 8th dorsal
IX	Disc between 8th and 9th dorsal
X	Intervertebral disc between 9th and 10th dorsal
XI	Upper half of body of 11th dorsal
XII	Middle of body of 12th dorsal
XIII	Lower half of body of 13th dorsal
LUMBAR	
I	Lower half of 1st lumbar, and disc between 1st and 2nd lumbar†
II.	Lower quarter of 2nd lumbar, and disc and upper quarter of the 3rd lumbar centre opposite disc†
III	Disc between 3rd and 4th lumbar
IV	Lower border of 4th lumbar
V.	Middle of 5th lumbar
VI	Lower quarter of 5th lumbar and disc between 5th and 6th
VII.	Upper fourth of 6th lumbar
SACRAL	
I	2nd fourth of 6th lumbar
II	3rd fourth of 6th lumbar
III	Disc between 6th and 7th lumbar

COCYGEAL —The cord tapers gradually to 3rd sacral vertebra

\* These nerves consequently run slightly forwards from the cord to leave the intervertebral foramina

† These nerves are directed slightly forwards on leaving the cord.

APPENDIX B—Table showing Persistent Electrical Difference between Surface and Cross Section. Distance between Contacts 1 centim Difference expressed in fractions of 1 Daniell

### I SCIATIC NERVE

#### (1) *In Connection with Brain*

Cat (71)*	018	Monkey (47)	007
(73)	013	" (217)	005
(75)	018	" (217)	006
(166)	008	" (221)	005
(273)	009	" (221)	006
(288)	008	" (262)	003
(290)	009	" (270)	003
(291)	004	" (280)	004
(292)	006	" (333)	005
(301)	004	" (333)	006
(301)	006	" (368)	005
(296)	009	" (368)	007
(296)	008	Average 005 Daniell	
(298)	01		
(298)	009		
(299)	009		
(299)	013		
(303)	009		
(305)	009		
(305)	01		
(382)	009		
(384)	0075		
Average 0094 Daniell			

#### (2) *Cord Divided in Dorsal Region*

Cat (32)	005	Cat (64)	012
" (36)	007	" (65)	013
(36)	007	" (206)	01
(157)	009	" (209)	012
(161)	011	" (209)	01
(164)	009	" (254)	011
(168)	008	" (263)	009
(172)	012	" (265)	008
(173)	011	" (267)	006
(175)	007	" (267)	007
(177)	008	" (275)	0085
(179)	008	" (276)	0125
(181)	011	" (311)	0125
(190)	01	" (312)	012
(200)	008	" (329)	01
(201)	011	" (329)	012
(203)	007	" (331)	008
(204)	008	" (331)	011
(363)	009	" (363)	007
Average 0094 Daniell			

\* As stated on p 303, the numbers in brackets following the mention of an animal refer to the page in our note ledger in which the observation is recorded.

*(3) After Previous Operations on Cord*

Cat (227) division of left posterior roots	007 left
„ (227) „ „ „	009 right
„ (230) division of right posterior column	008 left
„ (230) „ „ „	005 right
„ (247) „ „ „	012 right
„ (251) division of both posterior columns	012 right
„ (259) left hemisection	009 left
„ (259) „ „	008 right

## II. LUMBAR ROOTS.

*7th Left Lumbar Posterior Root*

Cat (341)	026	Cat (381)	018
(348)	02	„ (382)	016
(362)	02	Average 02 Daniell	

*6th Lumbar Posterior Root*

Cat (383)	011
-----------	-----

*6th Lumbar Anterior Root*

Cat (383)	0045
-----------	------

## III. SPINAL CORD.

ELECTRICAL Difference between Cross Section and Surface Cord Divided and Isolated at Position Indicated in Table. Contacts 1 centim. apart.

*(1.) Cord in Connection with Brain*

Cat (51) 1st lumbar	033	Monkey (41) 12th dorsal	018
(80) 12th dorsal	044	„ (48) 12th dorsal	024
„ (97) 12th dorsal	03	„ (52) 12th dorsal	029
(114) 2nd lumbar	037	„ (54) 12th dorsal	027
„ (118) 4th lumbar	04	„ (234) 12th dorsal	025
„ (124) 3rd lumbar	046	Average 025 Daniell	
„ (126) 2nd lumbar	04		
(288) 13th dorsal	033		
„ (308) 1st lumbar	033		
„ (314) 12th dorsal	025		
„ (315) 13th dorsal	032		
„ (317) 13th dorsal	032		
„ (319) 12th dorsal	029		
„ (323) 13th dorsal	031		
„ (324) 13th dorsal	033		
Average 034 Daniell			

(2) *Cord Severed from Brain.*

Cat (37) 8th dorsal	043	Monkey (271) 8th dorsal	017
„ (67) 9th dorsal	026	„ (281) 8th dorsal	027
„ (100) 9th dorsal	036	„ (321) 7th dorsal	013
„ (104) 9th dorsal	03	Average 019 Daniell	
„ (121) 11th dorsal	031		
„ (140) 10th dorsal	03		
„ (145) 10th dorsal	03		
„ (148) 11th dorsal	025		
„ (151) 10th dorsal	035	Cat (37) 2nd lumbar	035
„ (153) 11th dorsal	025	„ (124) 4th lumbar	033
„ (192) 11th dorsal	023	„ (170) 1st lumbar	029
„ (194) 10th dorsal	018	„ (243) 2nd lumbar	033
„ (196) 10th dorsal	03	„ (301) 1st lumbar	037
„ (243) 8th dorsal	025	„ (357) 2nd lumbar	036
„ (255) 8th dorsal	03	„ (366) 2nd lumbar	033
„ (289) 7th dorsal	014	„ (371) 1st lumbar	03
„ (327) 9th dorsal	028	„ (378) 3rd lumbar	028
„ (337) 6th dorsal	026	Average 033 Daniell.	
„ (339) 8th dorsal	03		
„ (344) 8th dorsal	04		
„ (346) 8th dorsal	026		
„ (349) 10th dorsal	02		
„ (355) 8th dorsal	04		
„ (375) 8th dorsal	039	Monkey (321) 2nd lumbar	018
Average 029 Daniell.		„ (232) 2nd lumbar	018

(3) *Cord in Connection with Brain, but divided Longitudinally into Right and Left Halves.*

		Left	Right
Cat (129)	2nd lumbar	029	018
„ (130)	1st lumbar	01	014
„ (133)	2nd lumbar	028	021
„ (135)	3rd lumbar	022	019
„ (309)	1st lumbar	018	027
„ (318)	13th dorsal	018	019
„ (324)	13th dorsal	015	022
Average 02 and 02 Daniell.			

		Left	Right
Monkey (213)	10th dorsal	02	014
" (215)	10th dorsal	023	012
" (217)	11th dorsal	013	011
" (235)	11th dorsal	013	011
" (237)	2nd lumbar	013	009
Average 016 and 011 Daniell			

(4) *Cord Severed from Brain and Divided Longitudinally.*

		Left	Right
Cat (137)	8th dorsal	007	016
" (143)	9th dorsal	021	013

(5) *After Section of Columns 1-3 Months Previous to Observation. Cord Severed from Brain.*

Cat (228)	division of posterior roots on one side, 11th dorsal	012
" (231)	division of right posterior column at 7th dorsal, 11th dorsal	025
" (252)	division of both posterior columns at 10th dorsal, 6th dorsal	022
" (260)	left hemisection at 9th dorsal, 4th dorsal	017
" (283)	left hemisection at 12th dorsal, 6th dorsal	038
" (228)	hemisection on right side at 9th dorsal, 1st lumbar	018
Average 022 Daniell		

(6) *General Average.*

Average, all cases, cord, Cat	032 Daniell
" " Monkey	022 "

## DESCRIPTION OF PLATES 29-35.

Plate 29 Arrangement of an experiment on a Cat for the investigation of electrical changes in the spinal cord consequent upon excitation of the peripheral nerves  
See Chapter III

Plate 30 Photograph of the encephalon and spinal cord of an adult Cat, two-thirds natural size, showing correctly the proportionate size of the various regions of the neural axis

The spinal nerves in this and the succeeding Plates are indicated by Roman figures and capital letters

*a, b, c, d* are points on the cortex cerebri referred to on page 329

Plate 31 Photograph of the neural axis in a Cat, the same preparation as in Plate 30, as arranged for the experiments on bilaterality, &c

Plate 32 Photograph of the encephalon and spinal cord of an adult Rhesus Monkey, to show, in comparison with Plate 30, the proportionate size and details of the neural axis in the Monkey as contrasted with the Cat.

Plate 33 Photograph of the neural axis in the Monkey, the same preparation as in Plate 32, as arranged for the experiments on bilaterality, &c

Plate 34 Photograph of a recent dissection of the lumbar plexus in an adult Monkey, showing the arrangement of the roots entering the plexus

*A c.* = Anterior crural nerve

*Ob.* = Obturator nerve

*E.P.* = External popliteal

*I.P.* = Internal popliteal.

*Hs* = Branches to hamstring muscles

*An* = Branches to anal and pudic plexuses

*\** = Filum terminale

Plate 35. Photograph of a recent dissection of the lumbar plexus in an adult Cat.  
Lettering as in Plate 34

*S.s* = Small sciatic.

VII *Some Points in the Structure and Development of Dentine**By J HOWARD MUMMERY, M R C S, L D S**Communicated by C S TOMES, F.R.S*

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[PLATES 36–39]

THE difficulties attendant upon the accurate microscopical investigation of enamel and dentine, especially of the latter tissue, have been so great, that very varied views as to their structure and development have been held up to the present time.

In the study of the development of dentine, where it is necessary to retain a very soft and delicate tissue, the pulp, in its natural relations to a hard, calcified tissue, the dentine the difficulties have been greatest, and it has generally been found necessary to resort to decalcification of the hard tissue by acids, to ensure this retention of the natural relations of the parts

Even, however, by this method, aided by the improved processes of section cutting now in use, good preparations, in which the cells of the pulp are retained in undisturbed contact with the dentine through any great extent of surface, are comparatively rare, and the cells of the pulp usually exhibit by their shrunken condition the injurious effects of the reagents used

It is probable also that there are other detrimental effects of these reagents present, which are not so easily detected, and the fact of the lime salts being removed from the dentine, does, as I shall endeavour to show, produce an alteration in its microscopical appearances

By a process elaborated by Dr L A WEIL, of Munich, and suggested to him by a method employed by Professor VON KOCH, of Darmstadt, in the preparation of Mollusca, the last-named difficulties have been overcome, and we can now cut preparations of the teeth with the pulps *in situ*, without decalcification. The process was described by Dr. WEIL in a paper entitled ‘Zur Histologie der Zahnpulpa’ (Leipzig, 1887), and in the ‘Zeitschrift für Wissenschaftliche Mikroskopie’ (vol. 5, 1888, pp 200–202), also by myself in the ‘Transactions of the Odontological Society of Great Britain’ (vol. 22, May, 1890).

The process consists, first, in “fixing” the soft parts by placing the freshly



extracted tooth in a saturated solution of corrosive sublimate in water—first dividing the specimen with a fine saw at one end to allow the solution to penetrate

When sufficiently fixed, the sublimate is removed by washing, and the tooth passed gradually through successive strengths of alcohol to absolute alcohol—it is then passed into chloroform, to which are gradually added fragments of dessicated Canada balsam, until a very thick solution of the balsam is produced. The preparation is then placed in a suitable receptacle over a water-bath, covered with more of the dessicated Canada balsam, and kept at a temperature of 90° C for several days, to allow the thorough penetration of the tissues with the hardened balsam.

The tooth is then removed, cut with a fine sharp saw under water, and the sections ground down, first on a lathe with corundum, and afterwards on a fine stone with water, under the finger. Staining in bulk may be accomplished during the treatment with alcohol, and the sections are mounted in chloroform balsam.

Very thin sections can be cut by this process, and good preparations exhibit a section of the whole pulp in undisturbed relation to the dentine, and, I think, with less alteration in the soft parts, than with any other process which has been made use of.

In the following investigation, the method above described has been employed, compared with, and controlled by, other specimens prepared by the more usual methods.

Of the various theories that have been held as to the development of dentine, the view most widely received, and embodied in all the principal text-books, is the conversion view of TOMES, WALDEYER, BOLL, and others, and given by Mr CHARLES TOMES, F.R.S, in his 'Dental Anatomy'

Certain appearances in fully formed, and in developing dentine, are not thoroughly accounted for on this theory, and I propose in the following communication to describe these appearances, as demonstrated in human dentine, in other Mammalian dentines, and in the vaso-dentine of fish.

These appearances I look upon as indicative of dentine tissue being formed by a connective tissue calcification, and thus being much more closely analogous in its manner of development to bone than has usually been supposed. Other observers have described appearances not fully accounted for under the current theories of dentine development, as will appear from the following brief summary, but no observer, so far as I am aware, has either described or figured specimens in such a way as to be at all conclusive; indeed, much that has been written on the subject scarcely amounts to more than an expression of *a priori* hypotheses.

Of the two different theories held, as to the method by which bone is formed from cells, the "conversion" view and that of "secretion," the former has been the most generally received.

According to the "conversion view" the masses of individual osteoblasts are consolidated by the deposit of lime salts in their substance, and the laminae of the

bone are made up of these layers of consolidated cells—the bone corpuscles are osteoblasts, which have become included in the calcified matrix, but have themselves remained uncalcified

The other view is that of “secretion”—the osteoblasts are held to secrete a substance which calcifies, and this secretion being not uninterrupted, but intermittent, the laminae of bone are produced

The layers of osteoblasts lying against the bone secrete the calcifying material, not becoming involved in the matrix themselves, with the exception of those which become enclosed by the forming bone and persist as lacunal cells

These two different views, with some modifications, have also been held as to the formation of dentine.

JOHN HUNTER held that the dentine was formed by a process of secretion, as the shell is by the animal that forms it. In ‘The Natural History of the Human Teeth,’ p 42, he says: “The ossified part of a tooth would seem to have much the same connection with the pulp as a snail has with its shell”

PURKINJE and RASHKOW held that the basis substance of the dentine originates from fibres which are formed by the dentine pulp—the dentinal canals representing the spaces between these fibres

SCHWANN considered that the fibres in human teeth run in the same direction as the canals, while PURKINJE and RASHKOW considered the fibres to be at right angles to the tubes (parallel to the surface of the pulp), and that the dentine was deposited in successive layers.

SCHWANN says: “We have to regard the dentine as composed of fibres (basis substance) between which the canals, possessed of separate walls, are present. But,” he asks, “in what relations stand the fibres and the tubes to the cells?” (odontoblasts), and he believes it possible that the dentine is the ossified substance of the pulp.

KOLLIKER, LENT, HERTZ, BAUME, look upon the formation of dentine as a secretion process, BAUME holding that “the odontoblasts secrete a material which calcifies, rather than that they are themselves converted.” WALDEYER, TOMES, BEALE, BOLL, and KLEIN, on the other hand, support the conversion view of dentine development

WALDEYER, considering the process of ossification to be identical with that of ordinary bone, holds that the dentinal fibres are the central remains of the odontoblasts, while their peripheral portions become basis substance.

TOMES (‘Dental Anatomy,’ p 170) says, “The dentine is, I believe, formed by the direct conversion of the odontoblast cells, just as the enamel is by that of the enamel cells, and is derived from them and from them alone.”

In a paper on the development of dentine and enamel read before the International Medical Congress, at Berlin, in August, 1890, Dr MICHAEL MORGENSTERN regards the hardening of the tooth as a transudation process, caused by a substance in the pulp itself which contains salts of lime independent of the odontoblasts, which sub-

stance is taken up by the odontoblasts, accumulates in them, and passes out of their peripheral border, &c, &c.

Professor KLEIN describes the dentine previous to its calcification as showing "just like the *substance* of the odontoblasts *the fine network of its matrix*." ('Atlas of Histology.') Again, in the 'Elements of Histology,' the same authority says "The dentine is composed of 1st, a homogeneous matrix, this is a reticular tissue of fine fibres impregnated with lime salts, and thus resembling the matrix of bone," &c, &c Professor KLEIN holds that the network of reticular tissue in the substance of the odontoblasts is the reticular basis of the dentine matrix, which is thus an *intra-cellular* substance By the aid of the mode of preparation of specimens above described, checked by the employment of other methods, I hope that I may be able to adduce more positive evidence of the *inter-cellular* nature of the dentine matrix than has yet been given, and to furnish something approaching to definite proof of the views herein set forth

A transverse, or longitudinal section of the pulp and dentine of a young healthy tooth, in which dentine formation is in active progress, cut by the process described above, shows the several parts with great distinctness. (Plate 36, figs. 1 and 2.) Owing to the retention of the lime salts, the fully calcified dentine is seen very clearly differentiated from the next layer (fig. 1, *b*), that "tissue on the borderland of calcification" (TOMES) which is situated between the fully calcified dentine and the odontoblast layer. The layer (*b*) which takes the stain faintly is traversed by the dentinal fibril and encroached upon above by the advancing line of calcification (*a*) in the form of coalescing globules and detached spherical masses

The odontoblast layer (*c*) is in immediate contact with the above-described semi-calcified layer (*b*) and the cells composing it lie square to the forming dentine In thin sections the odontoblasts form a single layer only, and in young teeth there is a distinct space between them (Plate 36, fig. 2.) Dr. L. A. WEIL ('Zur Histologie der Zahnpulpa') describes as a separate layer, a comparatively clear space existing between the odontoblasts and the general mass of the pulp tissue (Plate 36, fig 1, *d*), in which there are no cells, but interlacing fine fibres, which he describes as being in connection with the odontoblast cells. This layer takes the stain very faintly, or not at all, generally appearing with low powers as a clear zone immediately beneath the odontoblasts.

I can certainly corroborate the fact of the constancy of this appearance in the transverse sections of teeth I have examined, although not agreeing with Dr WEIL as to the ultimate destination of *all* these fibres. In some longitudinal sections, however, taken near to the growing and unfinished end of a bicuspid tooth, I have been unable to distinguish any such layer, the cells and fibres of the general pulp tissue being in immediate proximity to the odontoblasts. In transverse sections near the apex of the pulp (where the growth of the dentine is not very active) I have seen the layer much more marked than in other parts. Dr WEIL

compares this layer to basal membranes (*loc cit*) Beneath this is seen the "gelatinous connective tissue" of the main substance of the pulp with its numerous cells, blood-vessels, and nerves (fig 1, *d*)

In some of the first specimens which I cut by the balsam process (longitudinal sections of young healthy bicuspid teeth) my attention was arrested by a peculiar appearance at the border of the dentine which I had never seen in decalcified preparations

Processes were seen springing from the dentine, and blending with the connective tissue of the pulp, all round the margin of the pulp cavity (Plate 36, figs 3, 4, 5, 6). On examination with a higher power, these processes have the appearance of connective tissue bundles partially impregnated with lime salts in advance of the main line of calcification

At the inner margin of the dentine they are seen to spring from its substance in a direction more or less parallel to the surface, these horizontal bundles of fibres blending together into larger bundles at right angles to the surface of the dentine, much as the spreading roots of a tree coalesce to form its trunk

These bundles, the high refractive index of which suggests their partial calcification, are plainly seen to be continuous with the general connective tissue of the pulp In the specimen from which the photographs\* were taken, no stain was made use of, and in rubbing down the section much of the pulp was broken away from the dentine, rendering very conspicuous the connection of these fibres with the calcified tissue. I have not seen many specimens in which these connective tissue fibres gave evidence of partial calcification, and I am inclined to think the condition is an unusual one, although I have constantly, as described below, met with these fibres from the pulp incorporated with the portion of the matrix still unimpregnated with lime salts (One is reminded, by these specimens, of the similar appearances in the formation of bone in membrane, where spiculæ are seen shooting out in advance of the calcified substance)

The peculiar appearances exhibited by these specimens led me to examine other teeth for the same tissue, with the result that I found it was distinctly visible in the great majority of sections cut, the specimens above described being peculiar only in the large size and great apparent rigidity of these fibrous prolongations.

At the apex of the pulp cavity these processes are more slender, form wide, open loops, and can be traced for some distance into the pulp (Plate 36, fig 6).

In sections cut somewhat obliquely (not in the same plane as the odontoblasts) the appearance shown in Plate 37, fig 1, is often seen. Here small, deeply-stained cells, or cell-nuclei are seen, crowded upon, and following the course of, the bundles of connective tissue fibres, which in this specimen are very delicate. In other preparations, however, these bundles are much coarser, and the cells seem to be incor-

\* A set of photo-micrographs, illustrating this paper, are in the possession of the Royal Society. See p 543 *infra*.

porated in the bundles (Plate 37, fig 2), reminding one very much of the appearances in developing membrane-bone, where osteoblasts are seen applied to, and lying between, the bundles of osteogenic fibres

In the last preparation referred to (Plate 37, fig. 2), which is cut in the plane of the odontoblasts, their nuclei are seen in the interspaces of these bundles although the outline of the cells cannot be made out

A section which is not cut in the exact plane of the odontoblast cells exhibits the fibrous trabeculae with greater distinctness than one cut in that plane, although they can readily be seen among the odontoblasts in the latter preparations. I think this is accounted for by the fact that the stained odontoblasts lying among these fibres hide them to a great extent, but when cut obliquely, the odontoblast nuclei are seen end on, and the regular layer of cells not being conspicuous, the connective tissue bundles are more clearly seen

Many of the cells which are in contact with the processes above described, especially those which appear to be involved in the bundles, are distinctly smaller than the odontoblasts, and seem too closely applied to these bundles to be interpreted as odontoblasts. Associated, therefore, with these latter cells are other cells which, I believe, play an important part in dentine development, but they are destitute of processes, and not arranged in a definite layer

In longitudinal sections of teeth where the tubes are cut obliquely, or nearly at right angles, especially near the upper part of the pulp cavity, the reticular structure exhibited in Plate 38, fig 1, is sometimes visible, a fine net-work of fibres forming circular and oval meshes, involved in which are numerous small round cells. This appears to be the same reticulum of fibres described in the previous specimens, but seen, as it were, from beneath, the meshes being cut transversely

Having constantly found these appearances in fully-formed teeth, I proceeded to examine specimens which had uncompleted fangs, in which, towards the unformed apex, the deposition of dentine was in active progress

A longitudinal section from such a tooth exhibits the appearances shown in Plate 37, fig. 3.

In this rapidly growing portion of a tooth (Plate 36, fig 2), the odontoblast cells are seen to be disposed in a single layer, to lie square against the layer of stained, uncalcified matrix substance (Plate 37, *b*), which is here very broad, and to be distinctly separated from one another. This slight separation between the odontoblasts I have found to be very constant in young dentine. A distinct reticulum of fine fibres is seen passing between and enveloping the odontoblasts, and by careful focussing on the right plane (see Plate 38, fig. 3, *e*), these fibres can be seen to be gathered into bundles and incorporated with the matrix substance out of which they appear to spring.

Small elongated and irregular shaped cells are seen in this specimen, mingled with the odontoblasts. In this section also, as in others of very young dentine which has

not been decalcified, a faint striation parallel to the surface of the pulp cavity is visible in the recently calcified dentine

This striation cannot be seen in these specimens in the layer between the odontoblasts and the dentine, but in the same layer in the incisor of a Calf kept for a long time in chromic acid, it can be seen very distinctly.

The striation in the dentine is limited to a narrow area, the matrix at some little distance from the pulp cavity showing no indication of it, neither is it visible in the last-formed layers of dentine near the apex of the pulp cavity at this stage of development. It is particularly evident in the dentine of the Rat

Having satisfied myself of the presence of the connective tissue processes above described, in human dentine, I examined teeth of persistent growth, taking the incisor of the Rat (*Mus decumanus*)

A thin section, cut by WEIL's process, shows a very strong connective tissue in the pulp, and a very open meshed reticulum of connective tissue bundles at the margin of the dentine, covered with small rounded cells similar in appearance to those of the main substance of the pulp (Plate 37, fig 4)

In these specimens the incorporation of the connective tissue bundles with the forming dentine is particularly evident; the fibres, which form round and ovoid meshes at their point of junction with the dentine, lie in a horizontal or oblique position to the surface of the pulp cavity, and in many parts can be traced for a little distance into the substance of the formed dentine. Many of the small rounded cells seem to be incorporated with the fibres, as described above in human dentine, others are seen lying in the areolar spaces of the tissue

The strongest fibrous bands are usually seen at a little distance from the growing base of the tooth, and the whole of this tissue towards the apex of the tooth was apparently considered by Mr TOMES to be a degenerative tissue, as he says in the 'Dental Anatomy,' p 367, "near to the surface actually in wear, they (the fibrils) become cut off from the pulp cavity by the conversion of what remains of the pulp into a laminated granular mass, so that the dentine exposed on the surface of a rodent's tooth must be devoid of sensitiveness" I find, however, that in sections cut by the balsam process the pulp contains odontoblasts as far forward as it extends, and that in all the specimens I have examined the tubules of the dentine pass through this laminated layer to the pulp tissue, and are nowhere cut off from connection with it and its cells. One would imagine that in the process of preparing such teeth by decalcification, the boundary between the laminated dentine and the laminæ of the pulp tissue would be obscured, and thus lead to such an interpretation as the above

A very distinct striation of the dentine is noticeable at the margin of the pulp cavity, the individual striæ interlacing, but maintaining a general direction parallel to the connective tissue bands of the pulp which are incorporated with the matrix. These striæ are very visible for some way into the dentine, forming in this situation a



band of a slightly darker appearance than the rest of the dentine, and fading gradually away in the deeper parts of the tissue approaching the enamel. With good illumination the striæ can be detected in many parts in the form of fine lines in the deeper portion of the dentine. These markings bear a strong resemblance to those in a similar situation described above as sometimes seen in human teeth.

Allowing for the possibility of these connective tissue fibres being a degenerative tissue, I examined the growing base of the incisor of a young Rat, and found the same arrangement of fibres very distinctly blending with the dentine substance, and in this situation crowded with small polygonal cells, which in some parts were in such abundance that the septa seemed to be made up of cells (Plate 37, fig. 5).

The odontoblasts and the fibrous bands can in many parts be seen at the same time, but as in the case of the same tissue in human teeth, the fibres are most distinctly seen where the section is not cut exactly across the plane of the odontoblast cells.

In a molar tooth from a newly-born Rat, in which there was but a narrow strip of dentine formed, fine connective tissue fibres could be well seen running through the odontoblast layer to the dentine, and in some places forming loops at their junction with the dentine. Upon and around these are small cells, considerably smaller than the nuclei of the odontoblasts which are visible among them.

In some sections from the tusk of the Elephant, kindly forwarded to me by Professor MILLER of Berlin, I find a similar incorporation of the pulp tissue in the newly formed (tubular) dentine (Plate 38, fig. 2).

These specimens, however, having been prepared from dried pulps, do not exhibit the cells in their natural condition, although the passage of the connective tissue fibres of the pulp into the dentine is exceedingly well marked.

In the erratic deposits of secondary, non-tubular dentine, in the substance of the pulp of the tusk, so frequently met with, the incorporation of the stroma of the pulp in the tissue is very clearly seen (Plate 38, fig. 3).

At the suggestion of my friend, Mr. CHARLES TOMES, I examined the teeth of several fish in which an appearance of lamination is noticeable parallel to the surface of the pulp cavity, to discover if this same layer of connective tissue can be seen in vaso-dentine, between the formed dentine and the pulp. In the very characteristic vaso-dentine of the Hake (*Merlucius*), after many failures in consequence of the specimens not having been treated when sufficiently fresh, I obtained sections of these teeth showing a well defined layer around the pulp cavity, consisting of connective tissue fibres blending with the dentine, openings being present at intervals in this layer for the passage of the numerous blood-vessels (Plate 38, figs. 4 and 5).

In longitudinal sections these fibres are seen lining the pulp cavity from base to apex of the tooth; they are seen to be in close apposition to the most recently formed layer of vaso-dentine matrix, and have a very well defined limit towards the pulp.

The individual fibres when examined with a high power, are wavy in outline, many of them being somewhat flattened; they show a tendency to form arches with one



another, and the interval between the concavities of these fibres is often occupied by two or three curved ones passing from one side to the other. Their termination towards the pulp appears abrupt, but with high powers they are seen to be attached to the stroma of the pulp by delicate fibres. This layer is very closely applied to the blood-vessels, and in many places where a horizontal vessel traverses the pulp close to the dentine, these fibres appear to be attached to the vessel, or rather, it is involved in the meshes of the delicate pulp tissue passing from this layer to the deeper portion of the pulp. Here and there, one of the large flattened fibres may be seen to extend beyond the others, deeply into the pulp, there dividing into several branches. An unstained specimen shows very faint traces of cells near the dentine, but in those stained with carmine a layer of polygonal cells is visible in close apposition to the dentine. These cells vary much in size, they have a coarsely granular appearance, with a well-marked nucleus, and take the stain deeply. Near the base of the tooth they form a well-marked layer and are placed closely together (Plate 39, figs 1 and 2), but as the apex is approached they have a more rounded outline and less definite arrangement. Many of these cells have short processes (Plate 39, fig. 3) passing from one cell to the other, and here and there to the dentine, and very similar cells are seen scattered throughout the pulp.

From their close application to the dentine, their regular arrangement, and their strong resemblance to osteoblasts, I believe these cells to be intimately concerned in the calcification of the vaso-dentine matrix. At the base of the ankylosed tooth of the Hake, cells precisely similar in appearance are seen in contact with the surface of the bone.

In an important paper by Mr CHARLES TOMES "On the Structure and Development of Vascular Dentine," published in the 'Philosophical Transactions of the Royal Society' for 1878 (vol 169, Part I), he gives an account of the mode of development of this tissue which has since been generally adopted. The author describes a layer of odontoblasts as "clothing the whole pulp, and where there is a capillary at the surface they clothe it, so that when they calcify, the capillary becomes solidly imbedded in the dentine."

From an examination of the specimens which I have prepared, as described above, I am inclined to think that much of the tissue here called odontoblasts consists of the connective tissue I have alluded to.

Mr. TOMES has kindly lent me some of his specimens, preserved in balsam and in glycerine jelly. In these latter preparations the great majority of the processes attached to the blood-vessels are precisely similar in appearance to the fibres I have described. Mr TOMES notices in his paper that the oval nucleus of the odontoblast cells is in some cases very distinct, in others indistinguishable, and says "I have been unable to discover in what conditions this is the case." The explanation I believe is in the fact that in the teased-out specimens, the cells which play the part of odontoblasts lie here and there in the meshes of this connective tissue. Many of

the flattened fibres look very like cells, but are distinguished by the absence of a nucleus.

I think it is these fibres which clothe the blood-vessels that are in close apposition to them in their course through the pulp tissue, and it appears highly probable that in teasing out the pulp in any fluid medium, the blood vessels would be likely to draw away with them this layer of fibres from its attachment to the dentine.

In some transverse sections which were prepared by Mr TOMES and stained with hæmatoxylin, the layer of connective tissue fibres is deeply coloured, and where these are crowded together they look very like odontoblasts, but thin sections show them to consist of fine fibres and also show the absence of nuclei at their distal extremities.

While therefore agreeing with him as to the existence of an odontoblast layer in vaso-dentine, I think that the cells are very different in form to the odontoblasts of Mammalian teeth, bearing much more resemblance to osteoblasts, and that they lie in the meshes of, and are surrounded by a layer of, connective tissue fibres in intimate connection with the dentine.

These fibres form a much more definite and sharply defined layer than in any Mammalian teeth, so much so that they have been regarded by the above-mentioned author as a peculiar odontoblast layer.

After a reconsideration of his own and of my specimens, Mr. TOMES agrees with me that they must be considered to be of the nature of a connective tissue.

Some of his more recent investigations on the dentine of the Cod have a strong bearing on this subject. He finds an outer marginal layer of dentine in which bundles, like connective tissue bundles in a hyaline matrix, are plainly seen, springing from the deeper vascular part of the dentine, these fibres are arranged radially like those surrounding the pulp cavity. Also in transverse sections of the decalcified Hake's tooth the dentine is often seen split up into fine fibres, likewise arranged at right angles to the surface of the pulp cavity (Plate 39, figs. 4 and 5).

There still remains the not inconsiderable difficulty that the layer of connective tissue which I have described as surrounding the pulp of these vaso-dentine teeth, which is sharply defined and of great regularity, consists only of radial fibres, so that we are still no nearer to an explanation of the *concentric* striation of vaso-dentine.

As a result of the above observations I proceeded to examine teeth for evidences of lamination in the completed dentine, or for any indications of its having been developed on a connective tissue basis.

In corroboration of this latter point, connective tissue fibres are sometimes brought into view in the substance of the dentine in teeth softened by caries, the acid formed in the progress of this disease dissolving out the lime-salts.

Close to the inner margin of the dentine in a case in which caries had encroached upon the pulp cavity, the appearance represented in Plate 36, fig. 7, is visible. Here

the lime-salts and the tubules seem to have been dissected away, as it were, by the acid, exposing the connective tissue basis of the matrix.

As evidence of the completed dentine retaining something of a laminar structure, the following arguments may be adduced :—

1. Teeth decalcified by the mineral and other acids, break up at right angles to the tubes, that is concentrically with the pulp cavity.

2. Teeth partially decalcified by treatment for a short time with acids sometimes exhibit this splitting in a very marked degree

3. There is a faint appearance of striation (before referred to) in many teeth cut by the balsam process, this appearance being confined to the portion of the dentine which has been most newly formed, nearest to the active odontoblast cells in rapidly growing teeth

4 Mr. F. J. BENNETT, in a paper read before the Odontological Society in 1888,\* described the appearances produced by the action of glycerine on dentine in which laminae were brought into view

5. In several specimens of carious teeth, in the portion of dentine yet uninvaded by micro-organisms, but within the area of partial decalcification in advance of them, a minute striation is visible, bearing a very strong resemblance to the striation of voluntary muscular fibres, interrupted here and there by some rounded contours which it is somewhat difficult to explain.

6 In the vaso-dentine of fish, besides the lamination parallel to the surface of the pulp cavity, the dentine in decalcified specimens splits up at right angles to the pulp cavity, and bundles of fibres are seen following the same direction incorporated with the outer layers of dentine in the Cod (above referred to)

Now, unless it be held that these appearances have been brought into view by the processes employed, which I think can hardly be maintained by anyone who examines the specimens, the verification of these observations must lead to some modification of the ordinarily received views of dentine development.

We can no longer look upon the matrix of dentine as being a homogeneous substance, but must regard it as composed of a reticulum of fine fibres of connective tissue modified by calcification, and where that process is complete, entirely hidden by the densely deposited lime salts. These fibres decussate freely with one another, and I believe them to be analogous to the decussating fibres of bone. They are rendered visible in some instances by the slow decalcifying action of caries, as they appear to resist the action of acids more than do the lime salts.

For this layer of connective tissue surrounding the pulp and entering into the substance of the matrix I would suggest the term "odontogenic fibres," from their great similarity to the osteogenic fibres of bone. There are objections to the term osteogenic, as applied to these fibres in bone, as they are the scaffolding on which the bone is built up, rather than actually the genetic tissue of the bone, and the same objection

\* 'Transactions of the Odontological Society of Great Britain,' vol 21, November

holds good for the term odontogenic, but it is suggested as the most convenient appellation, and the one by which their analogy to the similar fibres in bone is best indicated

In the formation of sub-periosteal bone, bundles of fibres from the periosteum are seen springing from the bone, and in the alveoli formed between these bundles the osteoblasts lie.

These periosteal fibres penetrate the bone, and can be distinctly seen in it in many places, although the great majority of them are afterwards obliterated by absorption of the bone first formed, and the formation of dense bone around the Haversian canals—the so-called Haversian systems

A similar appearance is seen in cementum, the fibres being visible in this tissue as SHARPEY'S fibres. (Plate 37, fig 6)

The above investigations as to the occurrence of this tissue surrounding the pulp cavity in teeth, suggest the view that these fibres are the scaffolding on which the tooth matrix is built up—just as calcification proceeds in bone along and around the osteogenic fibres—that they are incorporated in the matrix of the dentine by calcification, and form really the basis of its substance

In the 'Dental Anatomy' (p 62), Mr TOMES says, "Several varieties of dentine exist in which those peculiarities of structure which differentiate it from bone are less marked, so that a point is sometimes reached at which it is hard to say whether a particular structure should more rightly be regarded as dentine or as bone. Hard or tubular dentine has always been considered least like bone in structure and in development"

Again, on p 176 (*loc cit*), speaking of the development of osteo-dentine, the same authority says, "With the exception of the thin external layers, which are developed from a superficial layer of not very highly specialised cells, osteo-dentine is built up in a manner fundamentally different from that in which hard dentine, plicar-dentine and vaso-dentine are constructed. . . . Its inner surface becomes roughened by trabeculæ shooting inwards into the substance of the pulp, which speedily becomes traversed completely by them, as well as by the connective tissue bundles which are continuous with them. Osteoblasts clothe, like an epithelium, the trabeculæ and the connective tissue fibres attached to them, and by the calcification of these the osteo-dentine is formed. The process is exactly like calcification of any membrane bone, and the connective tissue bundles remind one of those which are believed to be the occasion of the formation of Sharpey's fibres in bone"

The appearances in dentine which I have described in the earlier part of this paper, would seem to point to a mode of development of hard or tubular dentine which in many essential points tallies with the description of the development of osteo-dentine above given, and consequently presents a strong analogy to the development of bone in membrane.

In human dentine, as I have shown, trabeculæ are seen shooting inwards into the

pulp from the surface of the forming dentine. These trabeculæ (sometimes exhibiting an appearance as if stiffened by the deposit of lime-salts in advance of the general line of calcification) are continuous with the connective tissue fibres of the pulp.

These fibres and trabeculæ are also in the case of hard dentine, as in that of osteodentine and bone, covered with cells, which in many parts thickly clothe them, and which, it is to be supposed, have similar functions to osteoblasts. Smaller cells are intimately associated with the odontoblasts proper, the latter cells being also involved in the connective tissue stroma in continuity with the dentine, and according to the view which under the circumstances seems most reasonable, these cells together secrete a material which calcifies along the lines of the odontogenic fibres.

This view appears to be supported by the investigations into the development of vaso-dentine above recorded, for here the cells at the margin of the pulp cavity bear a strong resemblance to osteoblasts, and lie between and among the connective tissue fibres springing from the matrix, just as the osteoblasts lie between the connective tissue bundles in the calcification of sub-periosteal bone.

While convinced that the views I have advanced are correct as far as they go, I acknowledge that they render some things perhaps more difficult of explanation than do those ordinarily received, for example, the nature of the dentinal fibrils, their relation to the odontoblasts, and the share taken by them in dentine formation, were more easily explained upon the hypothesis that the matrix was formed by the direct conversion of a portion of the odontoblast. Further investigation into the contents of the dentinal tubes seems called for, indeed, the usually accepted view of the origin of the fibril has not appeared satisfactory to all observers. Professor KLEIN says, "However great the authorities who maintain that the cells of the outer stratum above referred to as the odontoblasts proper, send processes into the dentinal canals as the dentinal fibres, I must question the accuracy of this assertion, for I cannot find convincing evidence of those odontoblasts doing more than producing the dentine matrix. . . the dentinal fibres appear to me to be derived solely from the deeper layer of cells which are wedged in between the former"—'Atlas of Histology'.

The same view was maintained by Dr ANDREWS, of Boston, in a paper read before the IXth International Medical Congress at Washington.

My own observations on the relations of the dentinal fibril are as yet incomplete, many appearances met with being somewhat contradictory.

As pointed out by many observers, there is always present in developing dentine a layer of tissue between the odontoblasts and the fully calcified matrix which is "on the borderland of calcification," a tissue believed by those who hold the conversion view, to consist of the consolidated masses of odontoblasts prior to their calcification, but which according to the view of secretion here maintained, is a material elaborated by the odontoblasts and other cells upon a connective tissue foundation. It appears probable that this tissue being gradually saturated by the lime-salts elaborated by the cells, becomes supersaturated at a certain distance from the secreting cell, a

process analogous to crystallisation\* takes place, and the globules of calcoglobulin are deposited.

The calcification of the matrix of tubular dentine is so complete that the fully formed tissue appears to be perfectly homogeneous

A faint striation in newly formed dentine may, however, be detected, and is very marked in the incisor of the Rat before referred to, moreover, the effects of artificial decalcification and that caused by the progress of caries are such as to render visible this indication of lamination, and point to the original development of the matrix on a connective tissue foundation

To Mr CHARLES TOMES I am much indebted for the kind assistance and valuable suggestions he has given me throughout this investigation, and my thanks are also due to the Directors of the Marine Biological Association for the kind manner in which they have supplied me with fresh specimens, preserved by special methods.

#### NOTE.

Added March 5th, 1891

Since communicating this paper, I have received from Vienna a paper by Professor V. VON EBNER, which has a considerable bearing on the subject of the present communication. It is entitled "Histologie der Zähne mit Einschluss der Histogenese," and has been published recently in the 'Handbuch der Zahnheilkunde' now appearing in separate parts (Vienna, 1890-91)

Professor VON EBNER says "The dentine matrix appears to be homogeneous in sections ground in water, whilst in bone a fibrillar structure may be observed. If, however, dentine is decalcified with hydrochloric acid in a 10 or 20 per cent solution of common salt, one can detect in fine sections, or in thin pieces scraped off with a knife, a fibrillar structure. In pieces that have been torn off, we sometimes obtain the fibrillæ isolated. These fibres are exceedingly fine, scarcely more than  $5\ \mu$  thick" (the diameter of the dentinal fibril being from  $1\ 3\ \mu$  to  $2\ 5\ \mu$ ). "On the whole they are very similar to those of bone and also to those of fibrous tendinous tissues

"They swell up in alkalies and acids; they are uniaxial and double-refractive, in short, in everything they present the same characteristics as the glue-giving connective tissue fibres. The fibres, as in typical bone, are united into bundles about  $2\ \mu$  in diameter, not however arranged in lamellæ as in bone. The principal direc-

\* VON EBNER considers the optical characters of *Enamel* and its behaviour under the action of weak acids as strong evidence of its crystalline character. VON EBNER, 'Sitzungsberichte d Kaiser Akad d Wissenschaften, Wien,' 1889



tion of the bundles corresponds to the longer axis of the tooth, being by no means, however, parallel to it. On the other hand the bundles cross each other, and mostly in planes perpendicular to the dentinal tubules "

This author also refers to a laminar structure occasionally exhibited here and there in carious dentine, but he does not enter on the subject of dentine development or refer to any connection between the dentine and the connective tissue of the pulp, the appearances he describes, however, in formed dentine after decalcification will, if confirmed by other observers, go far to establish the truth of the views suggested in the present paper

### DESCRIPTION OF PLATES 36-39

#### PLATE 36.

- Fig 1 Human bicuspid tooth at age of 14 Transverse section of tooth and pulp prepared by WEIL'S method (a) Dentine, (b) layer of tissue "on the borderland of calcification", (c) odontoblast layer (the nuclei of several layers of cells visible), (w) the clear zone, with fine fibres, described by Dr. WEIL, (d) pulp, with cross sections of several blood-vessels Magnified 75.
- Fig 2 Human bicuspid tooth, which had been only partially erupted, the apex of the root not being completed. (a) The last calcified portion of the dentine, (b) the layer described by the same letter in fig. 1; this layer is much wider in proportion to the dentine than in teeth in later stages of development Magnified 250.
- Figs. 3, 4, and 5 Fibres springing from the dentine along the pulp margin of a Human bicuspid tooth, longitudinal section These fibres appear to be stiffened by calcification in advance of the mass of the dentine. Magnified 350.
- Fig 6 Fibres of the connective tissue of the pulp in continuity with the layer of the dentine which has not received its full deposit of lime salts; at the apex of the pulp cavity of a bicuspid tooth (Human) longitudinal section. Magnified 350
- Fig 7 Human molar tooth softened by caries, showing fibres in the substance of the dentine. Magnified 200.

#### PLATE 37.

- Fig. 1. Fine fibres in connection with the dentine on one side and the pulp on the other, which are here seen to be crowded with cells (or cell nuclei). Transverse section of pulp of crown of a bicuspid tooth (Human). Magnified 230



- Fig. 2 Human bicuspid Transverse section of the pulp of the crown Processes covered with cells. Larger cells lying in the spaces between these fibres, which appear to be the nuclei of odontoblasts Magnified 230
- Fig. 3. Human bicuspid tooth with uncompleted root Longitudinal section a short distance from the open end of the root (*d*) Dentine exhibiting indications of transverse striation, with the advancing line of rounded and globular masses of calcoglobulin, (*b*) the layer on the border land of calcification, (*e*) fine fibres of the pulp blending with the last layer of the dentine (*b*), (*o*) the odontoblast layer, not fully in focus, (*p*) the pulp, with its fusiform and other cells, some of which are seen lying among the odontoblasts Magnified 230.
- Fig 4 From a longitudinal section of tooth (incisor) of Rat (*Mus decumanus*) A narrow portion of newly-formed dentine at the growing base of the tooth. (*d*) Dentine, (*b*) uncompleted layer of dentine, (*f*) connective tissue incorporated with dentine, and in this position crowded with small cells. Magnified 230
- Fig 5 Incisor of Rat (*Mus decumanus*), longitudinal section at about the middle of the length of the tooth, (*d*) dentine showing very marked transverse striation, the general direction of these striæ being slightly oblique, in the same direction as the connective tissue fibres of the pulp (*f*) incorporated with the dentine Magnified 175
- Fig. 6. Cementum from transverse section of Human bicuspid tooth (*g*) Granular layer, (*s*) fibres of SHARPEY penetrating the outer layer of the cementum, (*p*) peridental membrane Reduced from Camera lucida drawing,  $\frac{1}{16}$ th oil immersion (POWELL and LELAND) Magnified 500

## PLATE 38

- Fig. 1. Human molar tooth, oblique section. Appearance of a reticulum of fibres at the pulp margin of the dentine forming very rounded meshes and studded with small round cells Magnified 350
- Fig 2. From transverse section of tusk of Elephant. (*a*) Ivory, (*c*) connective tissue of the pulp, prepared from a dry pulp (Dr. MILLER's specimen) Magnified 350.
- Fig. 3 Secondary deposit in pulp of Elephant's tusk. (*a*) The calcified nodule, (*c*) connective tissue of pulp. Magnified 350
- Fig. 4. Longitudinal section of tooth of Hake (*Merluccius vulgaris*), showing at (*d*) vaso-dentine traversed by (*b*) blood vessels, (*f*) layer of connective tissue fibres surrounding the pulp Magnified 150
- Fig. 5. Portion of the same more highly magnified (700 diameters), to show the connective tissue fibres (*f*), and their relations to the dentine (*d*), and to the pulp and blood-vessels (*b*)

## PLATE 39

- Fig 1 Vaso-dentine (*Merlucius vulgaris*), (*d*) vaso-dentine traversed by blood-vessels, (*c*) a layer of cells in close apposition to the dentine Magnified 350
- Fig 2 The same cells more highly magnified Magnified 700
- Fig 3 Some of the same cells at the base of the tooth, exhibiting processes Magnified 700
- Fig 4 From a transverse section of tooth of Hake, decalcified (Mr. TOMES' specimen), (*d*) vaso-dentine splitting into fibres, (*c*) layer of connective tissue fibres in pulp; (*b*) a blood-vessel. Magnified 75.
- Fig 5. From the same preparation as fig 4, more highly magnified Magnified 700.

DESCRIPTION OF UNPUBLISHED PHOTO-MICROGRAPHS DEPOSITED WITH THE  
ROYAL SOCIETY

## No I

- Fig 1 From a transverse section of a bicuspid tooth (Human), prepared by WEIL's balsam process, stained with borax-carminc (*a*) Dentine, (*b*) tissue "on the border-land of calcification", (*c*) pulp with odontoblast layer. Magnified 200 diameters,  $\frac{1}{4}$ -inch objective (SWIFT)
- Fig. 2 Transverse section of one cornu of the pulp of a young bicuspid tooth (Human). Magnified 75 diameters,  $\frac{1}{2}$ -inch objective, stained with borax carmine.

## No. II

Process or bundles of fibres which are seen to spring from the dentine (*a*) and in the calcified portion of which they appear incorporated; from the margin of the pulp cavity of a Human bicuspid tooth (age 14), unstained

- Fig 1 Magnified 200 diameters,  $\frac{1}{4}$ -inch objective (SWIFT).
- Fig. 2. One of the processes more highly magnified, 500 diameters, POWELL and LELAND oil immersion  $\frac{1}{16}$

## No III.

Other similar bundles from the same preparation Magnified 320 diameters, ZEISS apochromatic objective 3 mm., dry.

## No IIIA.

- Fig. 1. Similar bundles at apex of pulp cavity. Magnified 320.
- Figs. 2 (magnified 200) and 3 (magnified 75). From the middle of the length of the tooth.

## No IV

Fig 1 From the margin of the pulp cavity in the crown of a Human bicuspid (age 14) (a) Dentine, (b) fine fibres between the dentine and the main body of the pulp, crowded with nuclei near the dentine Magnified 320 diameters, ZEISS apochromatic 3 mm

Fig 2. Reticular appearance at the margin of the dentine in a Human molar tooth (longitudinal section), the dentine is cut obliquely, and viewed from beneath, numerous cells are seen upon the septa and lying in the interspaces Magnified 200 diameters,  $\frac{1}{4}$ -inch objective (SWIFT) (This preparation is not a suitable one for photography and is better represented by the drawing, Plate 38, fig 1).

## No V.

Human bicuspid tooth Transverse section. Showing processes in the pulp (b) connected with the dentine (a) and crowded with cells

Figs 1 and 2. Magnified 200 diameters,  $\frac{1}{4}$  inch (SWIFT).

## No VI

Figs. 1 and 2. Human tooth (bicuspid). Longitudinal section close to uncompleted apex of growing tooth, (a) Newly calcified dentine showing minute transverse markings, more plainly seen in fig. 3, (b) layer of uncalcified matrix (in this young condition of the tooth of great proportional width); (c) pulp with large odontoblast and other cells (In the photographs the objective has been focussed on the connective processes at the margin of the dentine, the odontoblasts being slightly out of focus) ZEISS apochromatic 3 mm. Magnified 320 diameters.

## No. VII.

Figs. 1 and 2. Longitudinal section of incisor tooth of Rat (*Mus decumanus*), (a) Enamel; (b) dentine, (c) lamination in dentine; (d) connective tissue of pulp incorporated in the dentine. Magnified 250 diameters,  $\frac{1}{4}$ -inch objective (SWIFT).

## No. VIII.

Fig. 1. Transverse section from tusk of Elephant, from a dried specimen, afterwards softened and mounted in balsam (Dr. MILLER's specimen). Magnified 320 diameters. ZEISS apochromatic 3 mm. objective.

Fig 2 Pulp-stone or secondary deposit from pulp of same tusk, showing the incorporation of the connective tissue of the pulp with this tissue (d) Dentine, (p) pulp. Magnified 320 diameters, ZEISS apochromatic 3 mm objective

## No. IX

Vaso-dentine Tooth of Hake (*Merlucius vulgaris*)

Fig 1. Longitudinal section (a) Vascular dentine traversed by blood-vessels, (b) layer of connective tissue fibres in contact with the dentine and lining the pulp cavity. Magnified 300 diameters, 4 mm apochromatic (ZEISS).

Fig. 2. From the margin of the pulp cavity at the base of the tooth of a Hake—showing cells, many of which have short processes lying upon the pulp surface of the dentine (a) Dentine with blood-vessels; (b) cells Magnified 320 diameters, 3 mm apochromatic (ZEISS)

## No. X.

Fig 1 Appearance of fibres in the substance of the dentine near the pulp cavity in a molar tooth (Human) softened by caries Magnified 200 diameters,  $\frac{1}{4}$ -inch objective (SWIFT)

Fig 2 Transverse splitting of human tooth at right angles to the tubes, caused by the action of formic acid. Magnified 175 diameters,  $\frac{1}{4}$  inch.

## No. XI

Fig 1 Root of Human bicuspid, transverse section. (a) Granular layer of cementum; (b) stained layer showing SHARPEY's fibres, (c) cells and tissue of peridental membrane Magnified 500 diameters, POWELL and LELAND  $\frac{1}{16}$ .

Fig. 2. Transverse markings in the dentine in caries within the zone of decalcification. Magnified 500 diameters, POWELL and LELAND  $\frac{1}{16}$  oil immersion.



VIII *Contributions to the Study of the Connection between Chemical Constitution and Physiological Action.*—Part II

By T. LAUDER BRUNTON, *M D*, *F R S*, and J THEODORE CASH, *M D*, *F R S*

Received March 2,—Read March 5, 1891

It is now more than four years since this research was begun, and it has necessitated such a large number of experiments that, if given in detail, they would fill several hundred pages, and, therefore, only a brief account of the results, with details of a few typical experiments, can be given here

During the time we have been engaged in this research a great deal of work upon the physiological action of aromatic compounds has been done by other observers, but upon trying to collate their results, with a view to arriving at some general conclusions, it appeared that the conditions under which the various experiments have been carried out have differed to such an extent as to render comparison very difficult

In this research we have endeavoured to perform our experiments as nearly as possible under the same conditions, so that the results should be comparable. We have employed bodies of comparatively simple constitution, so that differences in their physiological action might be readily connected with differences in their chemical structure.

#### PLAN OF THE RESEARCH

The plan of the present research to a certain extent resembles that of our former investigations into the action of the compound ammonias

We have studied

1st The alterations in action which occur when an atom of hydrogen in benzene is replaced by haloid radicles.

2nd. The action of the compounds formed when one, two, or more atoms of hydrogen are replaced by alcohol radicles.

3rd The alterations produced by the introduction of one, two, or three atoms of hydroxyl.

4th The alterations produced by the replacement of one hydrogen atom by the radicle  $\text{NO}_2$ .

5th. By the replacement of one hydrogen atom by the amidogen radicle ( $\text{NH}_2$ )

We have also examined the modifications in the action of various members of the series by changes in temperature

### GENERAL RESULTS.

The most marked actions of those members of the benzene group which we have examined were exerted on the spinal cord and brain. The action on the spinal cord was indicated by a tendency to tremor and the action on the brain by lethargy.

We observed certain differences in the symptoms, both motor and sensory, caused by various members of the group. We were struck by the fact that the symptoms they cause in Frogs bear a certain resemblance to those produced by certain diseases of the spinal cord in Man. Thus, benzene causes a tremor which seldom occurs but when movement is attempted, and in this resembles the tremor of disseminated sclerosis, whilst monochlorobenzene, moniodobenzene, and also amidobenzene cause the movements to assume a violent slapping character, which reminds one of the movements occurring in locomotor ataxy, a disorder in which the posterior columns of the cord are affected.

### METHODS

The methods employed were —

1st To examine fully the action of the various substances upon the system generally of certain animals (Rats and Frogs being chiefly employed), and

2nd. To study their effect in detail upon the brain, spinal cord, nerves, and muscles in Frogs, and on the circulation in Cats

### (1ST) GENERAL ACTION.

In the former class of experiments a known quantity of benzene or its compounds was injected in a state of emulsion into the dorsal lymph sac of a Frog or under the skin of the side of a Rat, and the progress of the poisoning observed

### OF EXAMINING THE (2ND, $\alpha$ ) ACTION ON THE SPINAL CORD.

If it was desired to test the irritability of muscle, spinal cord, and nerve, after the toxic symptoms had developed, the animal was decapitated and the various organs just mentioned were tested in the following manner — The upper portion of the spinal cord was exposed and stimulated by means of a faradic current of electricity, the electrodes employed having platinum tips terminated by short threads of silk moistened in blood serum and resting upon the cord. The action of the drug upon the excitability of the cord was judged of by the effect which stimulation of the cord had upon the muscles.



(2ND, *b* AND *c*) ACTION ON NERVE AND MUSCLE

The action on the cord having been ascertained, a preparation of the gastrocnemius and the sciatic nerve supplying it was made and placed in a moist chamber for examination. The nerve and muscle were then stimulated successively. Contractions resulting from single induction shocks were recorded upon a rapidly moving cylinder, and tetanic spasm of the muscle from stimulation by a faradic current was recorded on a slowly revolving cylinder.

(2ND, *d*) BLOOD-PRESSURE.

The apparatus employed in the blood-pressure experiments was somewhat complicated, as we endeavoured to arrange it so that we could take a tracing of the mean arterial pressure representing a long time in a small space, and yet obtain at any moment on a more rapidly moving surface such a tracing as would give an actual

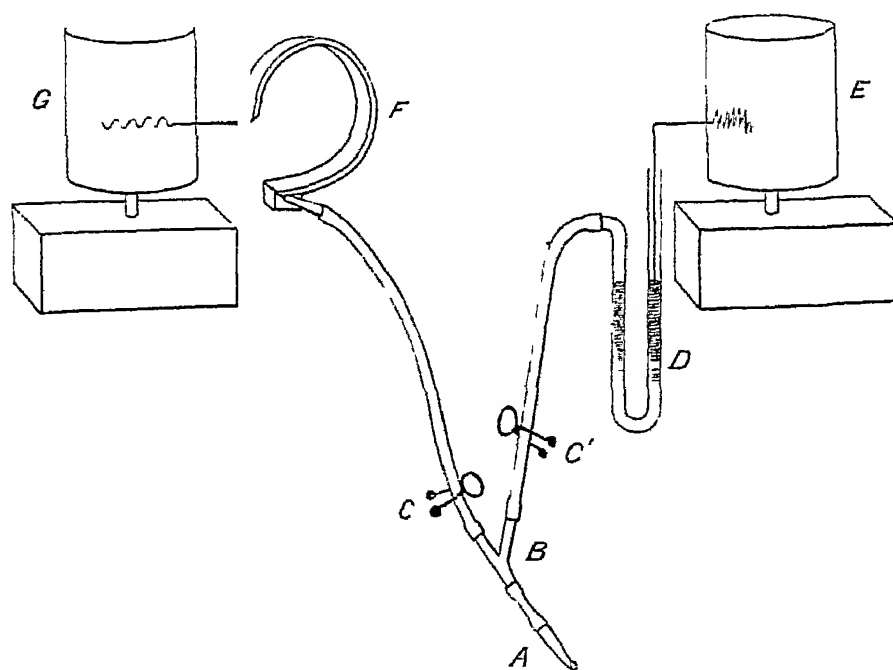


Fig 1 Diagram to illustrate the apparatus used in registering the blood-pressure, pulse, and respiration

*A* is the cannula for insertion into an artery *B* is a Y-tube by which the artery can be put in communication either with a mercurial manometer *D*, or a Fick's kymograph *F*, or with both of them at the same time *C* and *C'* are two clips by which the communication of either or of both manometers with the artery can be shut off at will *E* is a slowly revolving cylinder on which the mercurial manometer registers the blood-pressure *G* is a rapidly revolving cylinder on which the Fick's kymograph registers the pulse beats from time to time, and on which the respiration is also registered

indication of both the number and the form of the pulse beats and respirations in a given time This was accomplished by employing a mercurial manometer, which wrote on a blackened cylinder having a very slow speed of rotation (once in the hour), and in addition to this a Fick's spring manometer, which wrote upon a rapidly rotating cylinder. These manometers were capable of being clamped off from each

other, and the system of tubes leading to the Fick's manometer contained a very short length of thick walled india-rubber tubing, in order that the form of the pulse wave might be communicated as accurately as possible to the apparatus

This may be more readily understood by means of the accompanying diagram

At any time whilst the experiment was in progress, we were able, by clamping off the mercurial manometer and opening the clamp controlling the connection with the spring manometer, to obtain a tracing of the pulse unmasked by oscillation of the mercury in the former, which we could associate with the slow record by corresponding marks or figures. On the rapid drum we also registered the movements of respiration by means of a Marey's tambour, which was connected with a double tambour applied to the walls of the thorax.

#### SECTION I—ACTION OF BENZENE AND SOME OF ITS COMPOUNDS ON FROGS — GENERAL SYMPTOMS PRODUCED—ACTION ON SPINAL CORD, MUSCLE, AND NERVE

##### ACTION OF BENZENE $C_6H_6$ UPON *Rana Temporaria*

The general action of benzene on Frogs is to produce —

- (A) Lethargy and disinclination to voluntary movement;
- (B) Tremor and jerking, which always occur on movement, and sometimes to a slight extent when at rest,
- (c) Alteration in the response to stimuli, and
- (D) Subsequent paralysis.

The alteration in the response to stimuli observed in Frogs poisoned by benzene consists in —

- (a) Increased sensibility,
- (b) Diminished local movement,
- (c) General diffusion of movement

For example, when the toes of a normal Frog are pressed very lightly, it generally happens that no movement occurs at all, or only a slight local movement of the foot away from the stimulus. In a Frog poisoned by benzene, such a stimulus produces tremor, not only in the foot touched but over the body generally, while if the foot is withdrawn at all the movement is feeble and tremulous

##### *Effect of a Small Dose of Benzene.*

If one minim of benzene be injected into the dorsal lymph sac of a Frog, no marked symptoms are observed for from 15 to 30 minutes. At the end of this time, however, it is noticed that the leg, if gently extended, is drawn up with a tremulous or interrupted movement. This tremor develops further into jerking, which occurs

spontaneously and also whenever active movement, such as jumping or rising from the dorsal position, is attempted. This jerking may be accompanied by general movements of the trunk of a "ducking" or "huddling" character. There appears to be in most cases a temporary but distinct hyperæsthesia. This condition may appear exaggerated by attempted movement provoking tremor of the whole body. There are periods of complete rest between the attacks of jerking.

This is the usual extent of the symptoms exhibited by Frogs of 30 grms weight receiving one drop of benzene.

### *Effect of Larger Doses*

If a larger dose be injected, the inability to perform coordinate movement increases and at length the animal lies with the legs extended, a mere twitch of the toes and fingers only occurring on stimulation of the foot. Later on, the reflex becomes localised to the foot stimulated, and is ultimately lost altogether. The reflex from the eye is long maintained.

Absorption of benzene is slow and irregular, and it has been observed to cause a local rigor of muscle which may hinder absorption.

The heart usually continues to beat after reflex movement has ceased, or if it has stopped it is found to be still irritable.

### *Action on Individual Organs*

Destruction of the brain diminishes the jerking because it stops all attempts at voluntary movement, but if the Frog be left for a time till reflex movements are again active, the movements are to a large degree jerking. If the sciatic artery on one side be ligatured the jerking and tremor still occur on that side. This shows that the jerking is not due to a peripheral action of the drug on the motor nerves or muscles, but is due chiefly, if not entirely, to its action on the spinal cord. The jerking may sometimes be less on the ligatured side, but this is, we think, due to the effect of stasis in diminishing the irritability of the nerves and muscles on that side, although we cannot with certainty altogether exclude the possibility of the drug having acted as a peripheral stimulus. In a brainless Frog, which has been slightly poisoned by benzene, if the upper end of the dorsal cord be exposed and stimulated, the consequent contraction of the leg may be found less on the side of the unligatured artery than on the side of ligature, indicating that benzene has had a certain paralyzing effect on the nerves or muscles of the unligatured leg.

At a later period, stimulation of the cord is unattended by any contraction of the leg muscles on either side. This shows that the excitability of the cord is destroyed.

Stimulation of the nerve itself on the unligatured side yields a feebler contraction than on the ligatured, but even in cases of deep poisoning, reaction to some extent is

present This shows that either the motor nerve or muscle is enfeebled by this poison Figs. A and A'

The curve obtained by directly stimulating the muscle is strong, but often—as in the case of indirect stimulation—slightly longer than on the ligatured side. This shows that the muscle itself is somewhat enfeebled Figs. B and B'.

#### Action of Benzene on Muscle and Nerve

Decerebrated Frog weighing 22 gms Iliac vessels ligatured on the right side 2 minims of benzene injected into the dorsal lymph sac Examination of the muscles made 4 hours after the injection

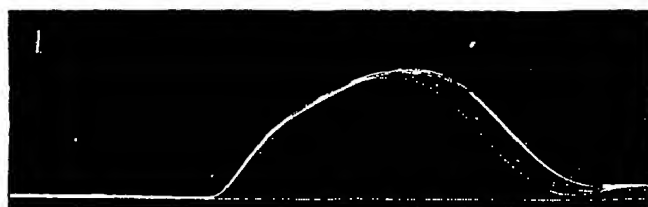


Fig 2 (A) Ligatured (*unpoisoned*) leg Curves obtained by repeated stimulation of *nerve*



Fig 3 (A') Unligatured (*poisoned*) leg Curves obtained by repeated stimulation of *nerve*

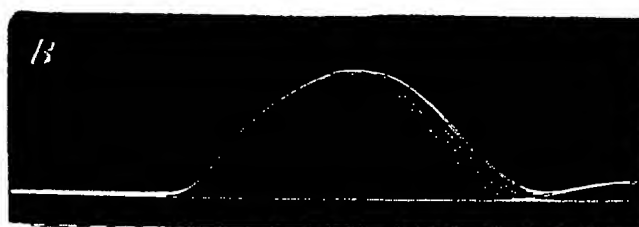


Fig 4 (B) Ligatured (*unpoisoned*) leg Curves obtained by repeated stimulation of *muscle* directly



Fig. 5 (B') Unligatured (*poisoned*) leg Curves obtained by repeated stimulation of *muscle* directly  
Time, 44 millims = 0 1<sup>s</sup>

The function of the heart is but little affected by benzene subcutaneously administered (Section II). The chief action of the poison is, therefore, on the spinal cord, though it has some effect upon the muscle substance, and also upon the terminations of motor nerves.

#### Alterations in the Action of Benzene by Heat and Cold.

The effect of heat is to increase the symptoms at first and then greatly to accelerate the occurrence of paralysis Thus, if a Frog be taken about an hour after the appear

ance of tremor, but while all reflexes are still active, and placed in a hot bath slightly below  $30^{\circ}\text{C}$ , in a short time all reflexes may have completely disappeared, while a control animal subjected to the same experiment still remains active. At a temperature of  $30^{\circ}\text{C}$  the reflex function of the cord of the Frog is suspended \*

Cold has no marked effect on the action of benzene, either in the way of accelerating or of retarding its action.

### *Experiment*

FROG Weighing 28 grms Room Temperature,  $63^{\circ}\text{Fahr}$ .

0<sup>h</sup> 0<sup>m</sup> One minim of benzene injected into the dorsal lymph sac  
 25<sup>m</sup> Weaker Slight tremor on jumping.  
 105<sup>m</sup> Much tremor on touching All reflexes "Ducking" movements No rigidity  
 170<sup>m</sup> Cannot crawl Draws the legs up with jerking movement Circulation active Pigment cell  
 much contracted Placed in a hot water bath at  $29^{\circ}\text{C}$   
 In 10<sup>m</sup> after immersion reflex had entirely ceased  
 In 15<sup>m</sup> ,, ,, the legs were in a condition of rigid extension  
 After removal from hot water, reflex tremor of the anterior extremities, trunk, and legs occurred  
 on irritating the foot On touching the eye, no closure of the eye but tremor of fore arms  
 and abdominal muscles occurred  
 (In benzene poisoning rigidity has been frequently noticed )

### *Result of Examination of Individual Organs*

Cord still irritable to slight extent. Muscles of thighs and upper part of gastrocnemius in rigor

## (1.) REPLACEMENT OF HYDROGEN IN BENZENE BY HALOID RADICLES.

Haloid radicles do not modify the action of benzene to the same extent as they do that of ammonia,<sup>†</sup> but nevertheless they do produce certain modifications, and in somewhat the same directions as we found in our experiments on ammonia

This modification is most marked in the case of iodine, whose compounds with benzene (like its compounds with ammonia) have a tendency to produce paralysis of muscle, of motor nerves, and of cerebral reflexes, without the production of spasm. It appears to possess a depressant action on the heart

Monochlorobenzene appears to affect the spinal cord greatly, causing spasm, and reflex action is more rapidly affected than after benzene. It diminishes the activity of the circulation, but it does not appear to affect motor nerves and muscles more than benzene.

The bromo- and iodo-compounds appear to differ from benzene and from chlorobenzene in the more powerful paralysing action which they exert on the cerebrum.

Weight for weight the chloro-compound is the most lethal, then the bromo-, and lastly the iodo-compounds

\* M. HALL, 'Roy. Soc. Proc.', 1831, p. 37

† BRUNTON and CASH, 'Phil. Trans.', 1884.

We shall now record three experiments selected as typical from others made with monochlorobenzene—the first at room temperature, the second under the action of cold, the third with heat

*Monochlorobenzene.* ( $C_6H_5Cl$ )

This substance causes in Frogs weakness, tremor, especially on movement, and inco-ordination of a character which reminds one of locomotor ataxy in Man. The circulation is little affected. The pigment cells are contracted

*Experiment*

*Rana Temporaria* of 24 grms. weight.

Nov 3<sup>rd</sup>

One minim of monochlorobenzene was injected into the dorsal lymph sac. Laboratory temperature 60° F

45<sup>m</sup> After injection. Slight tremulousness, both when attempting movement and when taken up

87<sup>m</sup> On stimulation of foot both legs thrown out in a "slapping" fashion, and there is much tremor and twitching of the head, limbs, and trunk. Frog crawls slowly and tremulously. Cannot hop. Kicking with legs is kept up for a long time (once for 20<sup>s</sup>) after stimulation of foot

100<sup>m</sup> It cannot crawl, can only draw the legs up with great labour and jerking. Circulation active. Pigment cells contracted to balls

130<sup>m</sup> The brain was now destroyed by pegging

135<sup>m</sup> Reflex is recovering, and there is slow withdrawal of the foot with great tremor. Tremor and some jerking still occur when no stimulation is applied

24<sup>h</sup> Next day it lies with its legs out. Any touch of the foot is followed by tremulous movements of the feet and hands, but no withdrawal of the leg.

On decapitating the animal and opening the lymph sac, it was found to contain some unabsorbed monochlorobenzene. The spinal cord was now destroyed from above downwards till reflex was almost gone. Much of spontaneous tremor now lost, but on pinching toe there was jerking of both legs

**ACTION OF COLD.**

Cold lessens the action of the substance, reducing the tremor and making the movement slower.

*Experiment.*

**FROG of 25 grms.**

0<sup>h</sup> 0<sup>m</sup>. One minim of monochlorobenzene was injected into the dorsal lymph sac after exposure to cold (7° C.) for 25 minutes

21<sup>m</sup> No tremor, but great lethargy. If taken out, it crawls forward very slowly, drawing the legs up with remarkable slowness

56<sup>m</sup>. Tremor is now distinct, though modified by the torpor of cold

96<sup>m</sup>. Distinct tremor to some extent, the frog feels markedly cold

130<sup>m</sup>. It makes springing movements, but does not change its position. Is much more normal than the Frog (similarly poisoned) at the room temperature, 60° F

- 146<sup>m</sup> As before. General lurching of the body is frequent  
 24<sup>h</sup> All reflexes are present, but slow and tremulous. Jerkings of limbs and lurchings of body whilst sitting still. On stimulating the foot the leg is withdrawn slowly and with a jerking movement. Circulation in the web is slow and unsteady. Vessels are dilated. Pigment cells contracted.

### ACTION of Heat.

Heat increases the action of the substance, rendering the jerking greater at first, and then rapidly lessening the reflexes, which are restored again by cold.

### *Experiment.*

#### FROG of 27 grms

- 0<sup>h</sup> 0<sup>m</sup> One minim of monochlorobenzene was injected into the dorsal lymph sac  
 65<sup>m</sup> Tremor on movement is now well marked  
 Frog was put into a hot bath at 29° C  
 Jerking at first was much increased, but soon became reduced  
 10<sup>m</sup> after immersion reflex is almost entirely gone, but there is still twitching on stimulation of foot (Control animal remains active) Seems to recover somewhat when taken out of the bath. It was again placed in hot water at 29° C  
 20<sup>m</sup> A slight tremor of the adductors was the only sign of reflex left  
 It was now placed in an ice chamber. Temperature, 7° C.  
 In 5<sup>m</sup> the reflex was much increased, some active spontaneous movements likewise occurred  
 30<sup>m</sup> after being placed in the ice chamber, reflex, though slow from cold, was active in all parts  
 Again placed in warm bath  
 In 15<sup>m</sup> all reflex was completely gone. It was now taken out and covered with ice  
 In 5<sup>m</sup> it was endeavouring to shake ice off  
 In 20<sup>m</sup> all reflexes were present, it drew its legs up strongly  
 Sits up well. All reflexes active and without tremor. Crawls well, does not attempt to hop  
 Next morning. After being 15<sup>m</sup> in bath at 29° C hops and springs well, and has, to a large extent, regained power of movement

#### *Monobromobenzene* (C<sub>6</sub>H<sub>5</sub>Br)

This compound appears to cause more lethargy and less tremor than chlorobenzene.

### *Experiment.*

#### FROG of 32 grms.

- 0<sup>h</sup> 0<sup>m</sup> Injected 1 minim of monobromobenzene into the dorsal lymph sac  
 40<sup>m</sup> The springs are only a few inches in extent. It hops along the bench if left to itself, but is somewhat lethargic  
 55<sup>m</sup> On touching the eye there is a start of the whole body.  
 85<sup>m</sup> It crawls. It can only spring from 2 to 3 inches at a time unless much roused. There is tremor in the limbs and trunk after a spring. Tremor is also provoked by tapping over the



- occiput or along the spine. A squealing sound occurs at intervals which appears to be due to strong contraction of the abdominal muscles, causing expulsion of air from lungs.
- 115<sup>m</sup> Circulation in the web is slow but general. Eye is prominent. Much tremor in all the limbs and trunk on attempting movement, which is now impossible.
- 180<sup>m</sup> Leg is drawn up weakly on irritating it. Frog seems, however, to be still hyperæsthetic. Some twitching of the muscles is noticed when movement is attempted.
- 275<sup>m</sup> Twitching and fibrillation of muscles on attempting movement, and also, but only to a slight extent, when lying still. There is no rigid spasm.
- 24<sup>h</sup> Cannot hop, but crawls. Very tremulous. Slow withdrawal of extended leg.
- 72<sup>h</sup> Tremulous on movement, but can take a series of short hops (2-3 inches), no tremor whilst movement not attempted.

### ACTION of Larger Dose (in brief)

#### *Experiment*

- 0<sup>h</sup> 0<sup>m</sup> The brain of a Frog weighing 35 grms was destroyed by pegging. The left sciatic artery was ligatured. The right sciatic plexus was divided. 3 minims of monobromobenzene were injected into the dorsal lymph sac.
- 45<sup>m</sup> Very faint reflex on stimulating the left foot by punching, no other reflex present.
- 80<sup>m</sup> As at 45<sup>m</sup>. Heart still beating.
- On stimulating the cord there was hardly any movement of left leg, and, of course, none of the right. The curve of contraction on indirect stimulation is somewhat lower and longer from the muscle poisoned by bromobenzene, than from that protected by the ligature.

### MODIFYING Effect of Cold (in brief).

#### *Experiment*

FROG of 32 grms. Room Temperature 15° C.

- 7<sup>h</sup> The Frog was placed in a cold chamber.  
3 drops of monobromobenzene were injected into the dorsal lymph sac.
- 40<sup>m</sup>. The Frog can crawl and hop short distances.

This Frog is much less affected than a control Frog poisoned by the same dose and kept at the room temperature.

### MODIFYING Effect of Heat

Heat may temporarily increase movement, but it lessens tremor and hastens disappearance of reflex action.

*Experiment*

FROG of 33 grms was kept for 20 minutes at a Temperature of 29° C 1 minim  
of Monobromobenzene Injected into Dorsal Sac

- 10<sup>m</sup> Temperature maintained Frog is crawling round the vessel There is an occasional powerful extension of both legs Head is "ducked" or depressed for an instant  
15<sup>m</sup> Eye-reflex gone, but the legs are still drawn up if extended  
30<sup>m</sup> Temperature maintained No withdrawal of the foot, and only slight tremor of the leg on pinching the toe Circulation is good, pigment cells are distended (Control Frog exposed to same temperature springs actively)  
35<sup>m</sup> Taken out of bath  
70<sup>m</sup> Reflex is returning Leg drawn up There are movements of respiration  
Put again into the hot chamber at 29° C  
76<sup>m</sup> Reflex has totally disappeared

*Condition of circulation, spinal cord, nerve, and muscles*

The Frog was now decapitated and examined

Heart was beating Stimulation of the upper part of the dorsal cord causes moderate contraction of the gastrocnemius This shows that the conducting power of the spinal cord is not destroyed

The curves obtained from direct and indirect stimulation of this muscle are good, though the altitude is somewhat reduced and the duration slightly increased

*Monoiodobenzene. (C<sub>6</sub>H<sub>5</sub>I)*

Monoiodobenzene causes lethargy with some increase of reflex Tremor occurs on movement, and spontaneous movements become much less sustained

*Experiment*

- 0<sup>h</sup> 0<sup>m</sup> Room temperature 65° F Half a drop of monoiodobenzene was injected into the dorsal lymph sac of a Frog weighing 36 grms  
35<sup>m</sup> after injection Lethargic, but springs well  
80<sup>m</sup> Springs strongly if roused, is torpid  
120<sup>m</sup> Legs are thrown out in a wild slapping fashion, extension is strong, but rather spasmodic  
155<sup>m</sup> On stimulation it gives a few active springing movements, which are tremulous and unsustained, and only move the animal a few inches  
195<sup>m</sup> Is now very tremulous on attempting movement, but not so when resting  
240<sup>m</sup> Still springs 1-2 inches Very tremulous Twitching of muscles occasionally noticed. Eyes protruded in breathing  
24<sup>h</sup> Lies on belly Withdraws legs slowly, but can hardly move, great tremor  
72<sup>h</sup> But little tremor now noticed, can hop repeatedly each movement very short, i.e., 2-3 inches

*Monoiodobenzene.**Experiment*

- 0<sup>h</sup> 0<sup>m</sup> 2 minims of monoiodobenzene were injected into the dorsal lymph sac of a Frog weighing 20 grms
- 5<sup>m</sup> Restless Breathing accelerated
- 8<sup>m</sup> Quieter
- 29<sup>m</sup> Quiet and lethargic If roused it is slightly tremulous
- 43<sup>m</sup> Reflex is increased Still lethargic Spring is short and tremulous
- 68<sup>m</sup> Reflex still increased All movements very tremulous Legs lie flat on the bench, the position of animal is low It still draws its legs up if they are extended When placed on its back, it can move round to the ventral position, but only with great effort
- 223<sup>m</sup> Still draws leg partially up, but very tremulously When placed on its back it tries to get round, but the only result is a twitching of the muscles of the limbs and trunk Eye reflex still present
- 278<sup>m</sup> Condition the same Heart accelerated
- 24<sup>h</sup> No respiration No reflex of any kind, but when the Frog is placed on its back there is a faint tremor of fore limbs

In another experiment the brain was destroyed in the first instance, the iliac vessels were ligatured on one side and 2 minims of monoiodobenzene were injected. The cord was destroyed just when the reflex movement of the ligatured leg was disappearing, the unligatured leg had ceased to respond some time before. During the destruction of the cord there was a twitch of the leg, the vessels of which had been ligatured. All the muscles were dark red and injected, excepting those of the ligatured limb Tetanus of the gastrocnemius on the poisoned side on stimulation of the nerve was weak and broken The muscle reacted more strongly to direct stimulation, but the contraction still was less active than that of the companion muscle on the ligatured side.

(2.) MODIFICATION OF THE ACTION OF BENZENE ( $C_6H_6$ ) BY REPLACEMENT OF ONE ATOM OF HYDROGEN BY AN ALCOHOL RADICLE.

The introduction of alcohol radicles into benzene in place of hydrogen appears to modify its action in much the same way as one would expect from a general consideration of the properties of the alcohol group, which, as a rule, have a sedative action on the nervous system.

The compounds of benzene with alcohol radicles produce less tremor, less hyperæsthesia, and greater lethargy than the halogen compounds

The circulation is but little affected by them.

These compounds, like the halogen compounds already discussed, exercise little action on muscle and nerve, but where an effect is observed it is greater on the nerve

The action of the alkyl compounds of benzene appears to be much more fleeting than that of the haloid compounds, the effect of the former generally passing off in 24 hours, while that of the latter often lasts two days or more.

In the case of methylbenzene,  $C_6H_5CH_3$ , a secondary increase of reflex action is sometimes observed after the reflexes have become greatly diminished and after spontaneous movement has quite disappeared. We have not yet been able to determine whether this is due to a paralysis of inhibitory centres in the brain, or to decomposition of the methylbenzene molecule with liberation in the organism of some product of its decomposition, having an exciting action, or whether it may be due to some other cause than these

This secondary increase in the reflex action of the cord is of some interest, inasmuch as a similar phenomenon, though much greater in extent, has been noticed by FRASER in the case of atropine. A further analogy between methylbenzene and atropine was observed in one case in which, after reflex action had become greatly diminished, convulsions of the fore legs with a certain degree of gaping and opisthotonos occurred in a Frog poisoned by methylbenzene

We shall illustrate the action of this drug by the notes of two selected cases of poisoning, in one of which the convulsive symptoms followed the course we have just described

*Methylbenzene*    $C_6H_5CH_3$    (*Toluene*)

Produces gradual failure of voluntary movement and reflex, accompanied by little or no tremor, occasionally convulsive movements of limbs and trunk occur.

*Experiment*

FROG of 38 grms   Temperature  $78^{\circ}$  F.

- 0<sup>h</sup> 0<sup>m</sup>   1 minim methylbenzene was injected into the dorsal lymph sac
- 27<sup>m</sup>.   Rather restless   Head rather dorsiflexed for a few seconds
- 35<sup>m</sup>.   If undisturbed will remain for a considerable time in one position   All reflexes are impaired, especially the eye reflex   Respirations 108 per minute
- 50<sup>m</sup>   Can spring if roused, but is generally perfectly still, will sometimes lie a considerable time with legs extended
- 53<sup>m</sup>   Moving about spontaneously
- 65<sup>m</sup>   Has had several attacks of convulsive extension of fore legs with throwing back of head and gaping, which have resulted in the body being propelled backwards   The left leg is slightly extended, the right quiescent.
- 80<sup>m</sup>   Lies with the legs in any position   Spasm not provoked by touching bell jar covering it, or by striking the bench, but occurs on pinching the foot.
- 125<sup>m</sup>   Circulation in the left web is very active   There is still some spasm in the fore arm   All reflexes are present to some degree, though the eye reflex is much impaired
- 24<sup>h</sup>   No tremor nor abnormality, except that the spring is short

*Methylbenzene**Experiment.*

DECEREBRATED Frog of 32 grms. Right Iliac Artery ligatured. Room Temperature, 69° F

- 0<sup>h</sup> 0<sup>m</sup>. 2 minims of methylbenzene were injected into the dorsal lymph sac  
 10<sup>m</sup>. All leg reflexes are present There is no tremor, Frog draws the leg up well  
 31<sup>m</sup> No tremor, it lies with its legs half extended Both legs are drawn up on touching, but more strongly on the ligatured side  
 71<sup>m</sup> All reflexes are gone Circulation in the left web is decidedly good, the pigment cells are contracted There is a very faint cardiac impulse still, just causing circulation in right web

*Condition of Spinal Cord, Nerves, and Muscles*

Distance of secondary from primary coil, 12 centims No contraction on stimulation of cord At 10 centims there is a twitch of both feet 8 centims tetanus of both legs (all tissues divided but the nerves) No contraction to speak of from nerve on the ligatured side, which seems exhausted by the few contractions caused by stimulation of the cord On direct stimulation of the muscle tetanus occurred at 16 centims

*Unligatured Leg*

There is no tetanus from the nerve, muscle tetanus with coil at 13 centims

This case, therefore, shows relatively little or no affection of muscle The nervous tissue is evidently the seat of the poisoning

*Action of Dimethylbenzene. C<sub>6</sub>H<sub>4</sub>2(CH<sub>3</sub>)*

Its action closely resembles that of the compound last described There is, perhaps, a little more tendency to tremor occasionally manifested. The heart is but little affected. The result of stimulation of nerve and muscle is the same as in methylbenzene. The only result observable on the day after injection is slight lethargy and a less vigorous spring than was executed before the administration of the drug

*Experiment.*

FROG of 32 grms

- 0<sup>h</sup> 0<sup>m</sup>. 1.5 minims of dimethylbenzene were injected into the dorsal lymph sac  
 5<sup>m</sup>. Breathing rapid Restlessness  
 32<sup>m</sup>. Spring short and weak, no tremor. Can get off its back  
 52<sup>m</sup>. Eye protruded, no longer closed on touching All reflexes are present Legs drawn up rather jerkily, cannot get off back  
 72<sup>m</sup>. Still faint twitch on pinching foot This is often, however, a mere fibrillation, with no true movement of the limb.  
 102<sup>m</sup>. All reflex quite gone. Circulation active Pigment cells contracted

*Condition of Cord, Nerves, and Muscles.*

On stimulating the upper end of cord there is a very faint twitch of the legs. Stimulation of the sciatic nerve gives a stronger contraction. Direct stimulation of the muscle causes more vigorous contraction. Heart beating strongly.

After a dose such as 1.5 minims, or even twice as much, has been administered to a medium-sized Frog, recovery usually takes place. In 24 hours, except for a little weakness and lethargy, the animal is scarcely to be separated from a normal Frog. There is no tremor. When equal doses of this and the preceding compound are severally administered to two Frogs of equal size, the action produced by the dimethylbenzene appears to be the stronger.

*Trimethylbenzene*  $\text{C}_6\text{H}_3(\text{CH}_3)_3$  (*Mesitylene*)

This substance appears to be the most active of the methyl compounds which we have investigated. The eye reflex is lost comparatively early, and, after a dose of 1.5 minims, all body reflex frequently disappears within an hour. After the eye reflex is lost, touching the conjunctiva not unfrequently causes movement of the limbs.

*Experiment*

FROG of 32 grms

- 0<sup>h</sup> 0<sup>m</sup> Injected 2 minims of trimethylbenzol under skin of belly  
 15<sup>m</sup> If laid on its belly, will lie still with the legs in any position. If put on its back, it may still make efforts to change its position, but they are not persisted in. No closure of eye on touching, but if touched there is extension of both legs. All circulation has ceased in web. No reflex on pinching, but occasionally 4–5 spontaneous extensions.  
 60<sup>m</sup> All reflex is quite gone.

*Condition of the Cord, Nerves, and Muscles*

On stimulating the cord there is feeble tetanus of both legs, which seems rather stronger in the ligatured. On the unligatured side nerve tetanus is moderately good with undulations. Muscle tetanus is less good, probably owing to exhaustion from previous stimulation through the nerve. On the unligatured side both nerve and muscle tetanus are as extensive when commencing as on the ligatured side, but are not so sustained.

(Circulation ceased early.)

The comparatively early cessation of reflex was noticed in almost all cases of poisoning by this drug.

Thus, one Frog of 48 grms. received 1.5 drops and another of 32 grms. 2 drops of trimethylbenzene. Reflex was gone in the former in 80 minutes, in the latter in 60 minutes. (Detailed results of reflex experiments are given in the next section.)

*Ethylbenzene*  $C_6H_5C_2H_5$ .

This substance is more active in causing paralysis than the methyl or dimethyl compounds, a slight degree of jerking may develop on attempting movement

If one minim of ethylbenzene be injected into the dorsal lymph sac of a Frog of 30 to 35 grms weight,

In 30<sup>m</sup> The frog appears to be weaker, but, if roused, may give a series of short slapping extensions of legs, which move the animal but a very short distance

„ 50<sup>m</sup> The ability to spring declines, attempts at crawling still occasionally occur. There is increasing apathy. No twitching whilst at rest, but muscular movements are rather jerking owing to failure of centres (nervous). Frog lies with legs out, but still starts if touched. Eye reflex persists as long as limb reflexes.

„ 100<sup>m</sup>. All reflex usually ceases, that in arms generally outlasting that in legs. Very occasionally a slight spontaneous start of legs occurs after all reflex has ceased.

Sometimes touching the eye may cause twitch of toes when all stimulation of foot is inoperative to cause reflex.

If the iliac artery be ligatured in a brainless Frog, the reflexes may appear rather more strongly on this side, but not invariably so, as often no difference is discernible.

The heart is usually found beating slowly, the ventricle is pale, and contracts imperfectly.

The circulation in the web may, however, cease at the same time as the reflex (as in one case 103 minutes after poisoning).

Stimulation of the cord (brachial) usually gives only a feeble contraction of both legs, not amounting to a tetanus.

In one case, 103 minutes after one minim of ethylbenzene, the cord was completely paralysed. In two other cases, when the poisoning took longer (150 minutes and 154 minutes), and a faint twitch still persisted as reflex, a distinct tetanus was obtained

If the iliac artery be ligatured on one side and poisoning carried to the abolition of reflex, the tetanus from the sciatic of the unligatured side is usually feeble or very feeble; that of the muscle is much stronger, but still somewhat impaired in contrast with the ligatured side.

In one case, after all reflex had gone, the cord still yielded tetanus without marked alteration in reaction from nerve and muscle on the unligatured side.



## Action of Ethylbenzene on Muscle and Nerve

Decerebrated Frog. Left iliac vessels ligatured 1 minim of ethylbenzene injected into the dorsal lymph sac

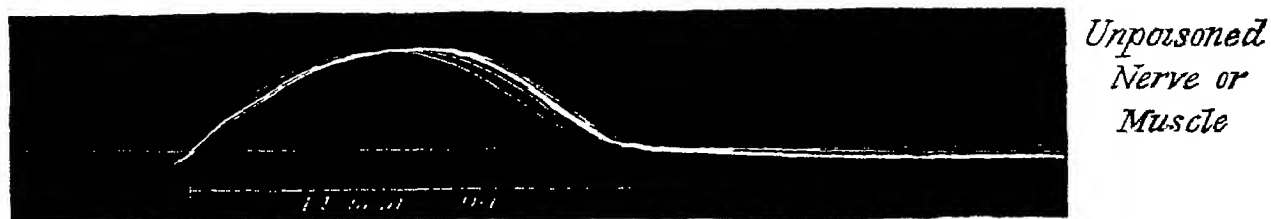


Fig 6. (a) Ligatured (*unpoisoned*) leg Twenty maximal stimulations of the sciatic nerve gave the above curves Direct stimulation of the muscle gave similar curves



Fig 7 (b) Unligatured (*poisoned*) leg Twenty maximal stimulations of the nerve gave the lower of these two series Twenty maximal stimulations of the poisoned muscle directly gave the upper series

Time 44 millims equal to 0.1<sup>s</sup>

*Experiment.*

FROG of 35 grms

- 0<sup>h</sup> 0<sup>m</sup> One minim of ethylbenzene injected into the dorsal lymph sac  
 43<sup>m</sup> If touched sharply will spring six or eight times very rapidly Spring is very short, but often repeated, and gives an appearance of great haste with but little progress  
 81<sup>m</sup> Cannot spring, but extension of legs is sharp and slapping, lies with legs out, no tremor or jerking, starts when touched; hyperæsthetic.  
 103<sup>m</sup> Reflex rapidly failing  
 140<sup>m</sup> All reflex quite gone, except slight tremor of foot on touching eye

*Condition of Cord, Nerve, and Muscles*

Stimulation of the cord gives a very feeble twitch of legs, but no true tetanus. On stimulation of the sciatic nerve the contraction is stronger, but still weak. Contraction from direct stimulation is very much stronger. Heart beating slowly, systole imperfect

TABULAR View of the Comparative Action of Benzene and its Haloid and Alkyl Compounds

Substance.	Motor symptoms	Time of occurrence	Circulation	Mode of administration	Duration of symptoms	Post-mortem examination
Benzene . . . .	Hyperæsthesia, starting, jerking on touching, and occasionally spontaneously	25 <sup>m</sup> to 30 <sup>m</sup> after injection of 1 minim	Not markedly affected	Injection subcutaneously Exposure to vapour	More than 24 hours	Local action—muscular rigor, cord chiefly paralysed Nerve affected to a lesser extent
Monochlorobenzene .	Hyperæsthesia, tremor on movement 20 <sup>m</sup> to 40 <sup>m</sup> after injection of 1 drop Jerking with withdrawal of foot on touching, ending in tremor without withdrawal Spontaneous jerking is interrupted if the Frog is pegged beforehand Kicking of the leg continues long after stimulation	20 <sup>m</sup> to 30 <sup>m</sup> after injection of 1 minim	As above	Injection subcutaneously Exposure to vapour Introduction into the stomach	Leg withdrawn (in 24 hours) slowly and with jerking movement	Cord generally capable of conducting to some extent Nerve affected to a lesser extent
Monobromobenzene .	Hyperæsthesia Broken movement, tremulousness Increasing weakness, twitching and fibrillation of muscles on attempted movement, but to a very slight extent spontaneously	As above	As above	Injection subcutaneously Exposure to vapour Introduction into the stomach	More than 24 hours	Cord as above Tetanus from it soon breaks down or yields clonus only Both nerve and muscle affected to a lesser extent
Monoiodobenzene	Hyperæsthesia, but less than is the case with Frogs poisoned by chloride or bromide Twitching and fibrillation as above Eye reflex seems to cease sooner	20 <sup>m</sup> to 80 <sup>m</sup> Develops later than the others	As above	Injection subcutaneously Exposure to vapour Introduction into the stomach	Action does not seem to outlast the bromide or chloride effect In this, as in others, heat of 29°C rapidly abolishes reflex after stage of excitement	As above The nerve and muscle seem to be relatively more affected

TABULAR View of the Comparative Action of Benzene and its Haloid and Alkyl Compounds—(continued)

Substance.	Motor symptoms	Time of occurrence	Circulation	Mode of administration	Duration of symptoms	Post-mortem examination
Methylbenzene	Usually no evidence of hyperæsthesia. All reflexes retained for some time. No spontaneous tremor, movements become weaker, and may be a little broken before reflex lost, but nothing like the weakness, jerking and tremor of the compounds above	30 <sup>m</sup> to 50 <sup>m</sup> increasing lethargy and weakness	Heart's action weak	Injection subcutaneously	Next day is usually lethargic, spring short, but no tremor or jerking observed	If the poisoning be very profound, the cord may scarcely conduct at all. The nerve is rapidly exhausted on stimulation. But voluntary motion and reflex appear to cease some time before conduction disappears
Dimethylbenzene	Symptoms as above, with perhaps a little more tendency to tremor, but this is still insignificant when compared with haloid compounds	30 <sup>m</sup> . Increasing weakness after injection of 15 minims. Reflex gone in 80 <sup>m</sup> to 100 <sup>m</sup>	As above	Injection subcutaneously. Larger doses than of haloids are needed to produce the symptoms	As in the case of methylbenzene	As above. There is still a weak tetanus from stimulation if poisoning has not been extreme
Trimethylbenzene	Restlessness succeeded by increasing weakness and lethargy. A little tremor present. Eye reflex is usually first lost. Stimulation from touching eye often causes leg movement. Most active of the three methyl compounds	20 <sup>m</sup> after dose of 15 minims. Eye reflex and all body reflex ceases in 30 <sup>m</sup> to 50 <sup>m</sup>	Heart often ceases soon	Injection subcutaneously. Stronger than above	As above	As above
Ethylbenzene . . .	No marked hyperæsthesia. There is increasing lethargy and weakness. No twitching when at rest, but muscular movements are rather jerking. Occasionally a spontaneous start of legs occurs after all reflex has ceased. Eye persists as long as limb reflex	50 <sup>m</sup> after 1 minim attempts at voluntary movement still occur. After 100 <sup>m</sup> all reflex has usually disappeared	Heart ceases about the same time as reflex or soon after	Injection subcutaneously	Shows a little weakness in 24 hours after poisoning	A weak tetanus may be obtained even when all reflex had ceased before examination

## (3) BENZENE WITH HYDROGEN REPLACED BY HYDROXYL (OH)

The introduction of the hydroxyl group in place of hydrogen increases the tendency to convulsions. These convulsions are due to the action of the drugs on the spinal cord, occur independently of voluntary movement, except when the dose is very small, and continue almost unchanged after destruction of the cerebrum. Slight tremor may occur before destruction of the brain, but is greatly masked by the powerful contractions referred to. Fibrillation to a limited extent is seen after the brain is destroyed. The action of the compounds containing hydroxyl differs with the number of atoms of hydroxyl present and their position in the benzene molecule.

In the case of monoxybenzene (phenol) the substance is identical whichever the carbon atom may be to which the OH group is attached in the benzene nucleus.

Experiments on this substance are so numerous that we have not recorded any here.

*Dioxy- and Troxybenzene.*

In the case of dioxybenzene there are three substances, ortho-, meta-, and para-dioxybenzene, having the hydroxyl groups in the positions 1:2, 1:3, and 1:4 respectively. The ortho-compound is usually known as pyrocatechin, the meta- as resorcin, and the para- as hydroquinone.

We may anticipate our description of the action of the one of these bodies—resorcin—by saying that its action, though differing in degree, is very similar in kind to pyrocatechin and hydroquinone, as was also clearly shown by BRIEGER\*. When .002 to .003 gram of the salt dissolved in a drop of distilled water is injected under the skin of the back of a Frog, in two minutes there is a certain amount of jerking observed in all the movements of the animal. This jerking rapidly extends to all the limbs and to the muscles of the trunk, so that in four to five minutes it has become universal. There is an occasional very short pause between the clonic movements, and not unfrequently at the commencement of their occurrence the animal emits a squealing cry indicating the involuntary expulsion of air through the larynx as a result of abdominal muscular compression. There is often gaping of the lower jaw. Reflex movement is increased for a time. Breathing laboured.

If the animal is confined under a funnel or bell jar open at the top the vessel becomes covered internally with foam. In ten to fifteen minutes the jerking movements become continuous, that is to say, not that they alter their individual character, but that they do not show any lasting intermission or rest pauses.

The animal is unable at the maximum of this condition to perform any coordinate

movement, whilst at an early period in the action of the drug all attempts at movement at once provoke and increase the clonus.

The jerking stage may last from one to five hours, or even longer. In the case of small doses it continues longer than after larger doses, which tend to cause paralysis. During this paralysis or semi-paralysis the extended legs are no longer drawn up on stimulating, though from a slight thrusting-out movement the reflex function of the cord evidently exists to some extent. There is more reflex activity in the anterior part of the cord than in the posterior part, occasional twitchings of individual muscles or groups of muscles still take place, but these are fainter than before, and scarcely affect the position of the limbs.

Recovery may occur, though it is rare, excepting in the case of large Frogs, after 0.03 gm. has been injected, but with smaller doses, before this paralytic condition has developed far, or after it has done so, the return to voluntary movement is often surprisingly rapid, though for some time jerkings and twitchings occur.

More usually the paralysis increases, and the legs remain extended in a semi-rigid condition, when all sign of life has disappeared.

If the dose administered hypodermically is as small as 0.0025 gm., very definite symptoms still appear in the case of small Frogs of 15 grms. weight. The power of voluntary movement is retained, but all movements become tremulous and jerking, and there is some tremor and incoordinate muscular contraction when the animal is not making any effort to move. The spring remains fairly strong, and slight hyperæsthesia is to be recognized.

In the course of seven or eight hours after the injection the animal is again practically normal. We have observed curious variations of reaction of individual Frogs equal in size, and which had been kept under exactly similar circumstances, towards resorcin, one animal appearing sometimes to be readily influenced by half the dose which produced little effect upon another.

Larger doses than 3 mg. accelerate the twitching and paralytic stage, absorption occurring readily.

Complete flaccidity with loss of all movement takes place. On destroying the brain and upper part of cord there may be total quiescence of all the muscles of the limbs and trunk during the operation, and frequently strong stimulation of the cord also fails to cause contraction. This shows that the power of the cord to conduct longitudinally is destroyed. The heart is generally arrested in diastole, but usually remains irritable, contracting two or three times after each mechanical stimulation.

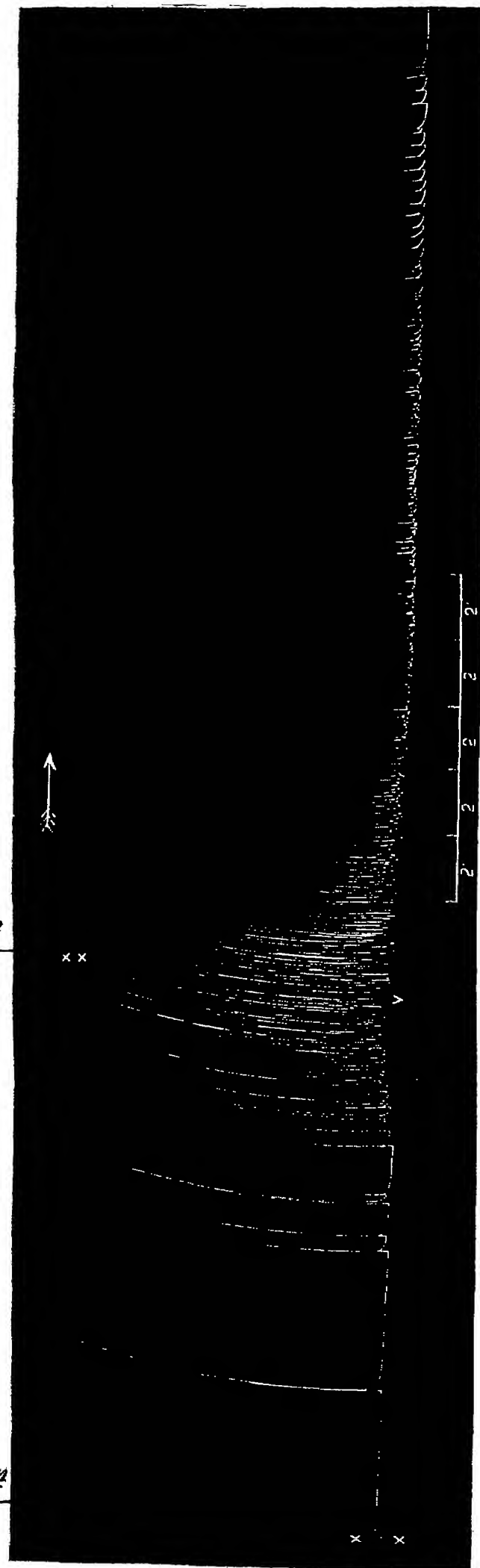
In advanced poisoning, which has not, however, taken place too rapidly, the function of the motor nerves is much impaired, and frequently that of the muscles also, and direct stimulation produces a stronger contraction than indirect.

The noticeable feature in the poisoning by dioxybenzene is the rapid development of muscular contractions, often occurring at very regular intervals of time, not passing into a tonic or tetanic contraction.

Fig. Action of Dioxylbenzene  $C_6H_4(OH)_2$  (1.3), Resorcin, on the Spinal Cord in causing Spontaneous Contractions of the Muscles.

0.04  
-Resorcin  
injected

-Curare  
injected



Frog weighing 37 grms Decerebrated The left iliac artery was ligatured and then all the tissues of the leg were divided, with the exception of the sciatic nerve The femur was fixed in a clamp, and the tendo Achillis attached to a lever At  $\times 0.04$  gm resorcin was injected in aqueous solution into the dorsal lymph sac At  $\times$  a large dose of curare was injected in the same way

All the contractions are spontaneous After the injection of curare they decline in amplitude from the paralyzing effect of the curare on the spinal cord. Time, 11 millims = 2<sup>m</sup> The tracing occupies 45<sup>m</sup>

This movement has its origin in the cord. The action of the drug eventually destroys the power of the cord to manifest increased reflex irritability by tetanic spasm when strychnine is injected, provided that this injection succeeds the full development of the symptoms produced by resorcin. If these, however, are but partially developed, tonic spasm results after strychnine. Curare injected into the dorsal sac abolishes these movements, the disappearance being noted first in the unligatured and later in the ligatured leg.

*Dioxybenzene 1 3 (Resorcin)*

ACTION ON FROG

*Experiment*

FROG of 24 grms

- 0<sup>h</sup> 0<sup>m</sup> Injected .002 gm dissolved in salt solution under skin of back  
 6<sup>m</sup> Restless Slight jerking  
 8<sup>m</sup> Jerking active and universal on movement  
 12<sup>m</sup> Short pauses only between jerking spasms Frequent squeal Reflex irritability is increased  
     Breathing laboured Gaping  
 24<sup>m</sup> Much froth round funnel from constant movement of animal Twitching and fibrillation of  
     muscles  
 1<sup>h</sup> Does not leave position, limbs chiefly in extension Jerking almost continuous  
 3<sup>h</sup>. Jerking diminished More successful effort at spontaneous movement From this time  
     improvement rapidly occurred.

*Experiment (in brief)*

FROG of 15 grms weight

- 0<sup>h</sup> 0<sup>m</sup> Injected .002 gm  
 8<sup>m</sup> Movements are distinctly tremulous Restlessness  
 17<sup>m</sup> Jerking of head, trunk, and limbs, legs flat at side of body, the animal resting on its ventral  
     surface throughout Froth in jar Cannot direct spring This animal is far more affected  
     than a Frog which has received twice the dose of trioxybenzene  
 37<sup>m</sup> Legs extended, and if pushed up revert to this position Also thrust out from time to time  
     Movements getting feebler, heart still beating No distinct eye reflex, but on touching eye  
     there is a twitch of the rest of body  
 67<sup>m</sup> No eye reflex, legs out Feebler movement of trunk and leg muscles still continue Increased  
     by stimulation and by putting in dorsal position. Heart beating  
 267<sup>m</sup>. No marked change of condition but twitching is now very feeble



*Experiment*

FROG of 18 grms

- 0<sup>h</sup>0<sup>m</sup> Injected .003 grm resorcin into anterior lymph sac  
 5<sup>m</sup> Violent jerking Ducking and squeaking now present (from contractions of abdominal muscles)  
 Frequent extension of limbs Movement constant  
 15<sup>m</sup> All eye reflex is gone Legs extended, there is twitching of groups of muscles, but the legs are but little moved  
 65<sup>m</sup> There are still twitchings of muscles but legs are not moved  
 120<sup>m</sup> All jerking ceased, legs appear to be in semi-rigor and yield no response to electrical stimulation

*Action on the Nerves and Muscles* —Resorcin is shown, by the rigor which occurs, to be a muscular poison, but it appears to weaken the peripheral terminations of motor nerves before affecting the muscles. This is shown by the following experiments.

If the brain is destroyed in the first instance and the iliac vessels on one side ligatured, reflex movement continues for a time more active upon the side of ligature, and the leg of that side reacts more powerfully to stimulation of the other, than the latter does itself.

The tetanus which the muscle yields on the unligatured side is feebler than on the other, the difference being more marked for indirect than for direct stimulation.

*Trioxybenzene*  $C_6H_3(OH)_3$  1 · 2 · 3 (*Pyrogallic Acid*) (*Pyrogallol*.)

This substance we found to differ decidedly, in its action towards Frogs, from resorcin. But the symptoms produced by it are not merely different in degree, but also in character

The tendency to the production of spontaneous rhythmical movements, which is so strong in the case of resorcin, is here much less marked. If, after a dose of .003 grm. has been injected an hour, the legs be gently extended, they are still drawn up, though with a somewhat tremulous movement. But little tremor or spontaneous jerking occurs if the Frog is not touched. Even when the brain is intact, there is not the same restlessness but rather a lethargic state, during which all reflexes are preserved for a time and then disappear, the eye reflex and that from the fore limbs being the first to go.

One of the most striking differences between resorcin and pyrogallol is that the former produces severe symptoms at first, from which the animal partially recovers, while the latter produces slighter symptoms at first but afterwards kills. (Thus an animal, poisoned by resorcin, may at first appear as if it would certainly die and yet recovers, while another poisoned with pyrogallic acid, may seem so little affected that one thinks it is in no danger, and yet it will be found dead next morning.)

The function of the cord does not appear to be quite so rapidly and profoundly

affected as in the case of resorcin, but the nerve was equally impaired in function. The muscle curve was usually well maintained but somewhat less extensive than before.

Whilst the immediate effects of the drug are much less marked than in the case of resorcin, it is certain that doses of over 0.02, though acting slowly, produce a highly deleterious effect on nutrition, as after them on the succeeding morning the animal was often found dead.

According to JUDELL, PERSONNE, and ZEISSER, the death in warm-blooded animals is due in large dose to action on the central nervous system, in smaller dose to the solution which is effected of the red blood corpuscles.

### *Experiment.*

#### EFFECT of a Small Dose of Pyrogallol. Frog of 15 gms weight

0 <sup>h</sup> 0 <sup>m</sup>	Injected 0.01 grm trioxybenzol (1 2 3, pyrogallol)
10 <sup>m</sup>	Restless. Movements rather tremulous
15 <sup>m</sup>	Spings well. But tremor on movement
35 <sup>m</sup>	Reflex is increased. There is no "huddling" movement
65 <sup>m</sup>	Is lethargic, but reflex increased. There is slight "squatting" or "huddling" movement occasionally
185 <sup>m</sup>	Spring rather short. Lethargic, tremulous on movement, but not when at rest. Reflex increased
300 <sup>m</sup>	Tremor less. Decidedly lethargic
	Next day, perfectly normal

### *Experiment.*

#### EFFECT of a Moderate Dose of Pyrogallol. Frog of 15 gms

0 <sup>h</sup> 0 <sup>m</sup>	Injected 0.02 grm pyrogallol into dorsal lymph sac
7 <sup>m</sup>	Restless. Movements somewhat tremulous
29 <sup>m</sup>	Crawls stiffly and with a little tremor. Spings. Has slight "hunching" or ducking movement of head. No foam in jar
42 <sup>m</sup>	Sitting up, springs well, though especially after movement there is tremor and "hunching" with bending of head, closure of eyes, apathetic
72 <sup>m</sup>	Crawls stiffly, more tremulous. Very little ducking or tremor when not attempting movement. Reflex is increased, striking bench originates movements. Gets off back with perfect ease. Is apathetic.
232 <sup>m</sup>	Condition continues much as at last report. It is only on movement that tremor and ducking occur. Spring short. Reflex increases. Is apathetic
353 <sup>m</sup>	Crawls well if roused and with less tremor, but is apathetic. No jerking if at rest. Next morning the animal was dead

*Experiment*

## EFFECT of a Large Dose of Pyrogallol

FROG of 15 grms

- 0<sup>h</sup> 0<sup>m</sup> Injected 0.075 grm pyrogallol into dorsal lymph sac
- 4<sup>m</sup> Restless Movements already tremulous
- 11<sup>m</sup> If roused makes rapid and violent series of springs, but only progresses  $\frac{1}{2}$ –1 inch at each movement After movement some involuntary extensions of legs and ducking of head
- 21<sup>m</sup> Resting on ventral surface Rarely starting occurs Reflex is increased Is lethargic Legs drawn up to body, and do not show rhythmical extensions as in case of dioxybenzol Still springs short distance, but feebly
- 54<sup>m</sup> Sits with head raised, and shows but rarely jerking or starting except when roused, can still crawl  
Cannot resume ventral position if placed on back
- 105<sup>m</sup> Weak, lethargic
- 160<sup>m</sup> Ducks and starts if roused Reflex is increased
- 275<sup>m</sup> Cannot get off back Much jerking if roused
- 400<sup>m</sup> Lies on belly, legs drawn up Attempts to spring, but hardly moves body Cannot rise from back
- Next morning was dead

*Experiment*

## ACTION of Pyrogallol on the Spinal Cord, Nerves, and Muscles

A brainless Frog with vessels ligatured in right leg About 0.12 grm injected into lymph sac After all reflex had entirely ceased the cord was exposed and stimulated by a faradic current It was found that at 15 centims distance of the secondary coil there was jerk of the right leg, and that on approximating the coil to 10 centims there was distinct tetanus on this side The left leg, which had been exposed to the action of poison, was not moved till the coil was more nearly approximated (3 centims) The tetanus of the ligatured leg was distinctly better than that of the unligatured from indirect, and slightly better from direct, stimulation

(In testing the effect of medullary stimulation, all the tissues connecting the legs with the trunk were divided excepting the sciatic nerves)

## COMPARISON BETWEEN THE ACTIVITY OF RESORCIN AND PYROGALLOL

In Frogs the activity of pyrogallol in the production of immediate symptoms appears to be only one-quarter to one-fifth as great as that of resorcin, ultimately, however, it is almost exactly equal in its lethal effect

## ACTION OF AMIDOBENZENE.

*Amidobenzene.*  $C_6H_5.NH_2$ . (*Anilin*)

In considering the action of benzene, in which one atom of hydrogen has been replaced by amidogen, we must remember that this substance, viz., anilin, is capable

of being regarded from two points of view (*a*) as amidobenzene, or benzene in which one atom of hydrogen is replaced by amidogen,  $\text{NH}_2$ , or (*b*) as phenylamine, *i.e.*, ammonia ( $\text{NH}_3$ ), in which one atom of hydrogen is replaced by phenyl ( $\text{C}_6\text{H}_5$ )

In correspondence with this constitution we find that we may regard the symptoms produced by it either as those (*a*) of benzene modified by amidogen, or (*b*) of ammonia modified by benzene. Thus we find the symptoms differ from those of benzene and resemble those produced by ammonia, in the tendency to more violent spasm and to greater paralysis of muscle and nerve. They differ from those of ammonia in the fact that the convulsions never assume the form of true tetanus, the tetanic spasm which the ammonia group would produce being broken up, so to speak, by the action of the phenyl

As contrasted with the compounds already discussed, with exception of the hydroxyl compounds, it will be at once apparent that the accession of symptoms produced by the action of amidobenzene is decidedly more rapid. Within 5 to 7 minutes of subcutaneous administration a distinct muscular twitching with incoordination of movement makes its appearance. The movements, whilst in the main purposeless and frequently confined to one side, have sometimes a regular speed of recurrence, one form of motion being repeated again and again at short intervals. Occasionally the thrusting out and flexion of one leg may cease and the corresponding limb will take up the same action and repeat the movement at a similar rate. Less frequently a group of movements more distinctly coordinate occurs, usually those observed in swimming, and they may persist for several minutes. The eye reflex appears usually to outlast limb reflex.

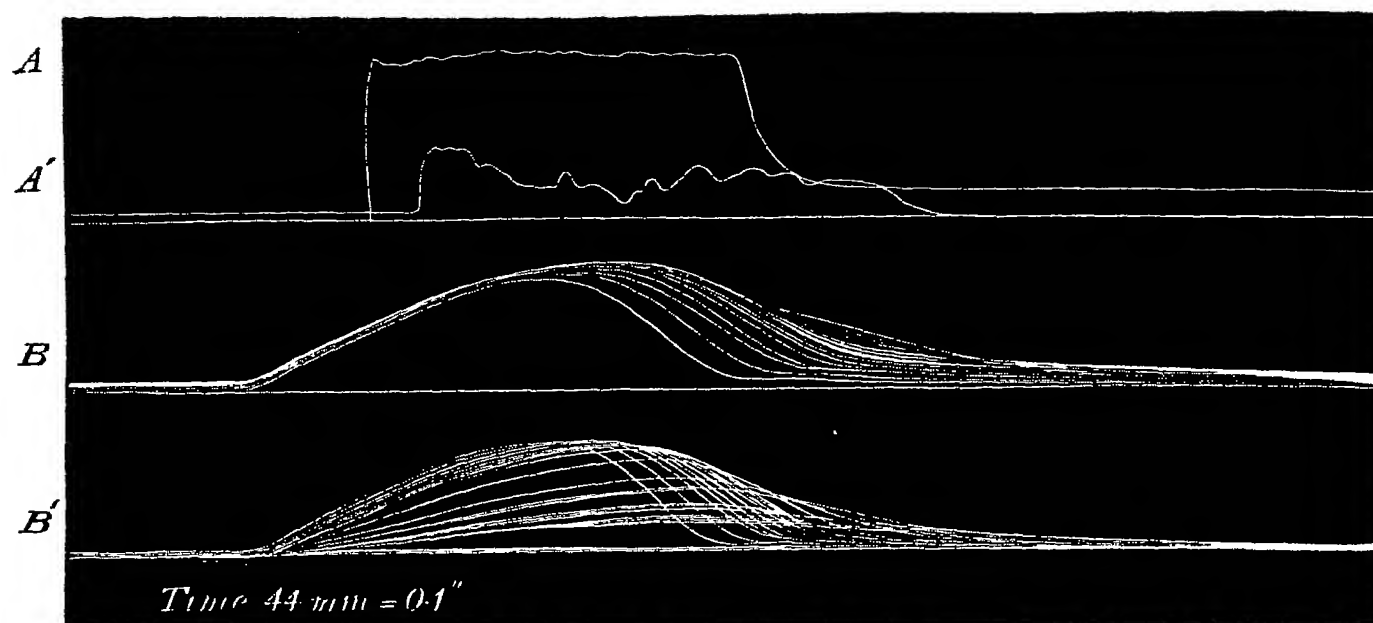
As the notes of the case quoted show, the longitudinal conduction of the cord is evidently diminished, and the effects of nervous stimulation are relatively to those of direct (muscular) stimulation greatly lessened, though the muscle is itself considerably affected by the poison.

It was evident from the examination of other animals which had not been so completely poisoned, that, even if the initial stimulation of the nerve yielded a moderately good contraction whether stimulation was repeated once or twenty times per second, the succeeding contractions became feeble and the muscle soon ceased to respond altogether to indirect stimulation.

When decerebration and ligature of the iliac artery had been practised before the introduction of the poison, it was found that reaction of the corresponding limb both to direct and indirect stimulation was stronger than on the side to which the poison had access by the circulation (Fig. 9, A, A').

At the same time tremor was observed in the ligatured leg, evidently as a result of central action of the drug, and the reflex from it was not longer maintained than on the unligatured side.

Fig 9 Action of Amidobenzene (Anilin) on Muscle and Nerve



A, tetanus from unligatured (poisoned) leg by direct stimulation for 5<sup>s</sup>

A' " " " indirect " " (i.e., stimulation of nerve)

B, thirty contractions at intervals of 2<sup>s</sup> from direct stimulation

B' " " " indirect "

The Frog weighed 30 grms. It was decerebrated, the left iliac vessels ligatured, and 1 minim of amidobenzene injected into the dorsal lymph sac. The examination was made after 2<sup>h</sup>. B and B' were taken before A and A'. The ligatured (unpoisoned) muscle gave on both direct and indirect stimulation a much more powerful and sustained contraction on tetanising, and the curve from single induction shocks did not elongate and fall in altitude as on the poisoned side (B').

### Experiment

#### ACTION of a Small Dose of Amidobenzene (Anilin)

##### FROG of 45 grms

- 11<sup>h</sup> 53<sup>m</sup>. Injected one minim of anilin into the dorsal sac
- 12<sup>h</sup> 3<sup>m</sup>. Active, but movements are tremulous, occasional quack
- 7<sup>m</sup>. Head tends to bend forward with jerk. All movements are now very tremulous. Moves round in circle, quacks. No springing spontaneously, but, if stirred, can still spring three or four inches. Breathing more laboured.
- 25<sup>m</sup>. Spasm chiefly in muscles of trunk at present. Crawling movement slow and tremulous, seems to feel ground with feet before resting on them. Still tends to creep round in circle. Can still spring five or six inches with great effort. Legs are drawn up slowly, and there is great trembling on alighting. The body gives a lurch when table is struck, but no tetanus.
- 40<sup>m</sup>. Quiet. All limbs drawn up normally. Seems more sensitive to cutaneous stimulation.
- 1<sup>h</sup> 0<sup>m</sup>. Quiet. Tremor on movement of body. Circumrotation. By rapidly approaching an object towards the eye, tremor of the whole body was produced, with or without a quack.
- 15<sup>m</sup>. Crawling is very slow and tremulous, and occasional spring of three to six inches.
- 2<sup>h</sup> 10<sup>m</sup>. No further symptoms. Crawl very tremulous, but stronger.
- 35<sup>m</sup>. Do. do
- 3<sup>h</sup> 10<sup>m</sup>. Hops better; is less tremulous.
- Next morning, perfectly normal.

*Experiment*

## MEDIUM Dose

FROG of 29 gms. Room Temperature, 63° F.

- 0<sup>h</sup> 0<sup>m</sup> Injected two minims amidobenzene into dorsal sac
- 7<sup>m</sup> Hind legs sprawl, toes spread out Twitchings in muscles Appears more paralysed in fore than hind legs Breathing laboured and accompanied by protrusion of eyes Leg at once drawn up if extended and gently touched Striking the bench on which the Frog rests provokes tremor of legs and all body
- 25<sup>m</sup> One leg extended, with twitchings and separation of toes, but devoid of rigidity The other leg and arm only show movements and twitchings, which are incessant Eye reflex still present (There is more movement here than in any other of the series)
- 27<sup>m</sup> Alternate extension and drawing up of right and left legs, as if in crawling, but no progress is made All movements are very jerking
- 33<sup>m</sup> Extremely active waving of arms, thrusting out of legs and jerking of body set in without any true tetanus, lasted 2-3<sup>m</sup> After this, slower swimming movements, which lasted 15-20<sup>m</sup> Thereafter movement (spontaneous) declined
- 137<sup>m</sup> Legs yield no reflex now Arms faint reflex Eye reflex still present Occasional spontaneous contractions of muscles of trunk and extremities still occur
- Examined There appears a slight coagulation at one part of dorsal sac
- Tetanic stimulation of cord produces a hardly observable effect Stimulation of the nerve gives broken tetanus Faradisation of the muscles gives sustained but small tetanic contraction The muscle gives a feeble curve

*Nitrobenzene (Mono)*

We have examined the action of only one nitrobenzene, namely the mononitrobenzene,  $C_6H_5(NO_2)$

Its action upon Frogs is that of causing lethargy, with increasing tremor on movement The power of voluntary movement disappears, touching the foot, however, may cause tremor of limbs.

Even when the Frog shows no reflex of any kind, a series of jerking movements of the legs may be made, apparently spontaneously, and these may be accompanied by muscular fibrillation

The circulation in the web is slow and feeble, the pigment cells contracted.

Recovery may occur from this condition.

In 24 hours there is ability to crawl for a short distance; the movements, however, are distinctly tremulous

When the symptoms of poisoning are fully developed, strychnine injected into the

doisal sac no longer produces tonic spasm, nor anything approaching it, but there is increased tendency to a diffused twitch in response to local stimulation

When the nitrobenzene is introduced into the stomach the same symptoms are induced, though more slowly than when the injection is subcutaneous

### *Experiment*

#### ACTION of Small Dose of Nitrobenzene on Frogs

After the injection of 1 minim of nitrobenzene into the lymph sac, in—

15<sup>m</sup> to 20<sup>m</sup> Movement is tremulous, legs more slowly withdrawn Occasional starting in limb when lying quiet, but usually no tremor during rest Occasionally a series of rapid extensions of legs, as in swimming, occur Reflex decreases till at 80<sup>m</sup> there may be only twitching without withdrawal of foot

If 2 minims are injected, the symptoms may develop more rapidly Eye reflex may disappear in 40<sup>m</sup> to 50<sup>m</sup> It may be outlasted by extension of legs as a reflex act

#### *Effect of Heat, 30° C*

In a Frog poisoned by nitrobenzene and kept at 30°, the symptoms were as follows —

- 5<sup>m</sup>. Tremor well marked
- 10<sup>m</sup> If leg is pinched it is thrust out and drawn up There may be a coordinate kick with both legs No withdrawal of arms if pinched, but legs are moved
- 35<sup>m</sup> All reflex is entirely gone, except the faintest tremor on pinching either of the feet If taken out and placed on the bench there may be soon slight return of reflex, but this is usually very slight

#### *Effect of Cold, 7° C*

- 50<sup>m</sup> After injection of 1 minim, still hops Some tremor and slowness in drawing leg up after spring
  - 80<sup>m</sup> All reflexes present Has quite ceased to crawl
  - 200<sup>m</sup>. All reflexes present No tremor when not attempting movement
- From this condition complete recovery occurs

#### *Effect on the Spinal Cord, Nerves, and Muscles*

When reflex has almost entirely ceased it is usually found that stimulation of the upper part of the cord causes a very faint twitch in either leg (even if the sciatic artery has been previously tied in one) On the unligatured side indirect stimulation caused a very feeble contraction, if any, direct stimulation a relatively stronger, though imperfect contraction, which becomes rapidly prolonged on frequent repetition of stimulation (fig. 10) On the ligatured side both direct and indirect stimulation yielded good contractions The chief effect is on the cord, which is markedly paralysed by this drug, especially in its conducting power Next to this the end plates of the nerves are paralysed, and lastly, the muscular



## Action of Nitrobenzene on Muscle and Nerve

Decerebrated Frog weighing 24 grms Right iliac vessels ligatured 0.05 c.c. nitrobenzene injected into the dorsal lymph sac Curves taken 5<sup>h</sup> after the injection



Fig 10 Muscle of ligatured (unpoisoned) leg Stimulated by opening shock of induction coil every 2<sup>s</sup> Curve obtained by stimulation of the nerve was nearly equal to that obtained by direct stimulation



Fig 11 Muscle of unligatured (poisoned) leg Stimulated in the same way The muscle relaxes imperfectly during the intervals between the contractions There was no response at all of the muscle when the nerve was stimulated

*DA in 1 second*

*Experiment*

MEDIUM Dose of Nitrobenzene. Frog of 29 grms

- 0<sup>h</sup> 0<sup>m</sup> Injected 2 minims of nitrobenzene into dorsal lymph sac  
 24<sup>m</sup> Torpid and slower in movements  
 34<sup>m</sup> Rests on belly, does not sit up, crawls and springs, but movements are tremulous and legs not rapidly drawn up Repeated springing movements  
 50<sup>m</sup> All reflexes present, but the leg is drawn up slowly and jerkily No tremor on movement whilst lying still, except an occasional starting of limb  
 79<sup>m</sup> Suddenly executed series of 10 to 12 rapid extensions of legs as in swimming No eye reflex  
 84<sup>m</sup> Sharp twitch of both legs without withdrawal on pinching foot, but no movement of arms or trunk Very faint reflex of each arm on stimulation of itself Circulation very active, pigment cells not markedly altered  
 109<sup>m</sup> Movements of leg muscles very faint

*Action on Spinal Cord, Muscle, and Nerve*

Exposed the brachial cord Left leg entirely divided except sciatic nerve, no contraction on tetanising nerve or cord Response to direct stimulation of the muscle was extremely feeble, stronger in the other leg, from which 90 contractions were taken

## EXPOSURE TO VAPOUR OF THE BENZENE COMPOUNDS.

The original experiments of BRIEGER,\* who showed how readily poisoning in Frogs might be induced by placing the animals in solutions of resorcin and its isomers, demonstrated the fact that by cutaneous absorption these substances are highly lethal. CHRISTIAN† has demonstrated in the same manner the poisonous action of benzol. The literature of pyrogallol abounds with instances of poisoning produced by the application of the drug applied in the form of ointment to the human body. The inhalation and cutaneous contact of the vapour of nitrobenzene have caused poisoning, and anilin when brought into contact with raw surfaces, as in the treatment of skin diseases, and more especially when its vapour has been inhaled, has produced its characteristic poisonous effects. Exposure of Frogs to the vapour of the anilins and their alcoholic combinations has been found by JOLYET and CAHOURS‡ and other observers to cause poisoning.

In confirming these and other experiments, we have found that exposure of Frogs to the vapour of benzene, its haloid compounds, its alcoholic compounds, to anilin, and to nitro-benzene, produces the characteristic symptoms of poisoning with great rapidity and completeness. We introduced Frogs into large funnels, the lips of which were covered with vaseline, so that they fitted air tight upon glass plates. In the neck of the funnel a fragment of sponge was contained, and into this the body to be tested was dropped. There was by this method no actual contact of the substance with the Frog, merely the exposure to the vapour liberated from the sponge.

We will merely quote one or two of such experiments in this place.

*Experiment*

## ACTION of the Vapour of Monochlorobenzene.

FROG of 15 grms. in large funnel as above described    Temperature 15° C

- 0<sup>h</sup> 0<sup>m</sup>    Dropped three drops of monochlorobenzene into the sponge contained in mouth of funnel
- 20<sup>m</sup>    Violent springing alternating with crawling movements, great frothing on sides of funnel    Legs are strongly withdrawn
- 45<sup>m</sup>    Movements, much less powerful, are jerky and broken
- 85<sup>m</sup>    All reflexes are jerking    Start of body and limbs on striking bench    Lies still if not roused, legs extended
- 95<sup>m</sup>    All movement completely gone    *Frog taken out of the funnel*
- 135<sup>m</sup>.    There is a very faint twitch of toes on stimulating fore foot or hind foot    On decapitating, a

\* BRIEGER, 'Arch. f. Anat. u. Phys.', 1879.

† 'Comptes Rend.', vol. 56, p. 1131.

‡ 'Zeitschrift f. Physiol. Chemie,' vol. 2, p. 282.

weak movement of arms and legs occurred. On stimulating the spinal cord, contraction in legs was very imperfect and unsteady. Nerve distinctly impaired in function. Muscle gives feeble tetanus. Heart still beating slowly.

### ACTION of the Vapour of Dimethylbenzene

The symptoms produced by dimethylbenzene were much less marked, chiefly characterised by motor paresis.

### ACTION of the Vapour of Amidobenzene (Anilin)

Anilin caused, after an initial period of excitation, great tremor and twitching, and after exposure to vapour for 40 minutes, the animal hardly possessed the power of crawling. Appearances like those of paralysis agitans.

### *Experiment.*

### ACTION of the Vapour of Nitrobenzene

PLACED a Frog under glass on filter paper. Temperature 15° 5 C

- 0<sup>h</sup> 0<sup>m</sup> At upper end of glass, five drops of nitrobenzene dropped on sponge  
 20<sup>m</sup> Cannot hop, all reflexes present, but slow and jerky. Breathing rapid  
 60<sup>m</sup> *Decerebrate*. Thereafter no spontaneous movement causing tremor occurred, but on irritating foot, withdrawal was very slow and still tremulous  
 420<sup>m</sup> All reflex gone from legs. Very weak reflex from arms. Circulation active, strong

### *Condition of Spinal Cord, Muscle, and Nerve*

Decapitated, prepared upper part of cord and cut through all tissues but nerve of one side. Contraction in gastrocnemius of this side, though not so strong as of the other on stimulating cord. After contraction occurred, fibrillation lasted some time.

Although it may seem almost superfluous after what we have already said, yet we shall now give, in the briefest possible manner, the most prominent results obtained, which may serve to contrast the bodies we have examined.

*Benzene* (aromatic) causes relatively but little tremor except on movement, and whilst it may for a time increase the reflex function of the cord, in the end it causes paralysis. The central nervous (cerebral) apparatus is somewhat specially affected by *bromobenzene*, whilst spontaneous jerkings, with tremor on movement and increasing lethargy, characterise *iodobenzene*. *Monochlorobenzene* tends to cause more pronounced spasm than the foregoing. There is great tremor, with ataxic movements. The circulation is but little affected.

The *methyl compounds* abolish voluntary movement and ordinary reflex, but sometimes after the ordinary reflex response has disappeared, touching may cause other movements which are not usually induced, as touching eye causing extension of limbs, but no eye reflex (as in case of trimethylbenzene), occasional clonic convulsive movements of limbs and trunk have been observed to occur spontaneously (as in case of methylbenzene). There is more tremor after dimethylbenzene than after methylbenzene. The eye reflex disappears relatively soon.

The trimethylbenzene is distinctly the most active of the three

*Ethylbenzene* is stronger than methylbenzene in producing paralysis, but not so strong as the trimethyl compound. Some amount of tremor is observable on attempted movement.

*Dihydroxybenzene* meta (resorcin) is distinct from all the others in the spontaneous, rapidly occurring, and somewhat rhythmical movement which it occasions. This symptom, whilst rapid in making its appearance if the dose is small, lasts for a long time before paralysis of the cord ensues.

*Pyrogallol* has not the same tendency to cause clonic spasm, but tends rather to produce a lethargic state with gradual decline of reflex.

*Amidobenzene* causes the most rapid occurrence of motor phenomena, the hydroxyl compound excepted. There is great tremor after a spring. Very active incoordinate movement is made, but tonic spasm is absent.

*Nitrobenzene* causes lethargy with increasing tremor on movement. The reflex is abolished somewhat early, but after this time a series of jerking movements of the legs, perhaps with fibrillation, may be observed.

## SECTION II—ACTION OF BENZENE AND ITS COMPOUNDS UPON REFLEX

An extensive series of observations was made with the view of testing the effect upon reflex action of the various bodies entering into the series under discussion. Decerebrated Frogs, prepared some time previously, were used for this purpose.

Immediately before the experiment commenced, the right iliac artery and vein were ligatured, in order that an estimate might be formed of alteration of reaction originating, not in the cord itself, but in the muscles and peripheral nerve terminations. The foot of the suspended Frog was stimulated by dilute acid of various strengths, from 1 per 1000 to 1 per 6000 (by measure). The reflex was tested every 10, 15, or 20 minutes, according to circumstances, and estimated by means of a metronome beating half-seconds.

The time of withdrawal was recorded, and from the figures obtained the diagrammatic charts were constructed. One difficulty peculiar to the substances under consideration was met with, namely, that from the action of certain of them, a condition of spontaneous jerking was developed, which was aggravated by immersion, even in pure distilled water, at the moment the application was made. This action, which occurs when the foot is very suddenly immersed, but not nearly so much so when gradually, was specially pronounced in the case of benzene, monochlorobenzene, and amidobenzene (anilin). The difficulty was overcome by a more gradual immersion, and by repeating the test until the uniformity of time of withdrawal clearly indicated that this was due to the stimulation by the acid.

On account of the motor symptoms produced by the hydroxyl compounds, we found them unsuited to this form of experiment.

The ultimate effect of many bodies in the series is to render the withdrawal of the foot highly tremulous and jerking. The flexion of the leg is followed by an extension, and this again by another flexion, so that instead of a sustained withdrawal from the irritating acid fluid, the foot is splashed in and out, and the action is continued until the foot is washed with pure water, and sometimes even after washing. After use the animals were placed in the cold and kept moist. The doses employed throughout the series of over 70 experiments were either the  $\frac{1}{36}$  of a cubic centimetre, or exactly double the quantity. The measurement was made in an accurately graduated capillary tube. Twenty-four hours after the larger dose reflex was still active, chiefly in the case of Frogs receiving the moniodobenzene, dimethylbenzene, and benzene, though with the smaller dose it was usually retained, excepting after trimethylbenzene.

*Benzene*     $C_6H_6$

This body in larger dose,  $\frac{1}{18}$  c c rapidly lengthens the time elapsing before reflex reaction to acid solutions, which were previously strong enough to cause rapid withdrawal of the foot. The curve which may be obtained by placing verticals, representing the time elapsing before reflex withdrawal of the foot, upon an abscissa, which is divided into equal time intervals, shows a parallel change of responses on the ligatured and unligatured sides, allowance being made for the slower reflex in the former owing to blood stasis. With a smaller dose,  $\frac{1}{36}$  c c, the failure of reflex is much more gradual, in the experiment from which the curve is formed it varied only from 1.5 second to 7.5 seconds in the course of  $4\frac{1}{2}$  hours. There was no certain indication of shortening of the reflex phenomenon even at an early stage of the poisoning.

We quote the results of two experiments \*

\* In recording the reflex time we occasionally give two speeds, as 1 second to 1.5 second, indicating at that particular time a withdrawal, sometimes at 1 second, sometimes at 1.5 second. In the figures we have drawn up the mean is given between these numbers.

*Experiment a* (4)

FROG of 32 grms, pegged some hours previously

LIGATURED Right Iliac Vessels. Acid Solution 1-4000 (by measure) Reflex three times tested at short intervals Injected  $\frac{1}{18}$  c c. Benzene into Anterior Lymph Sac

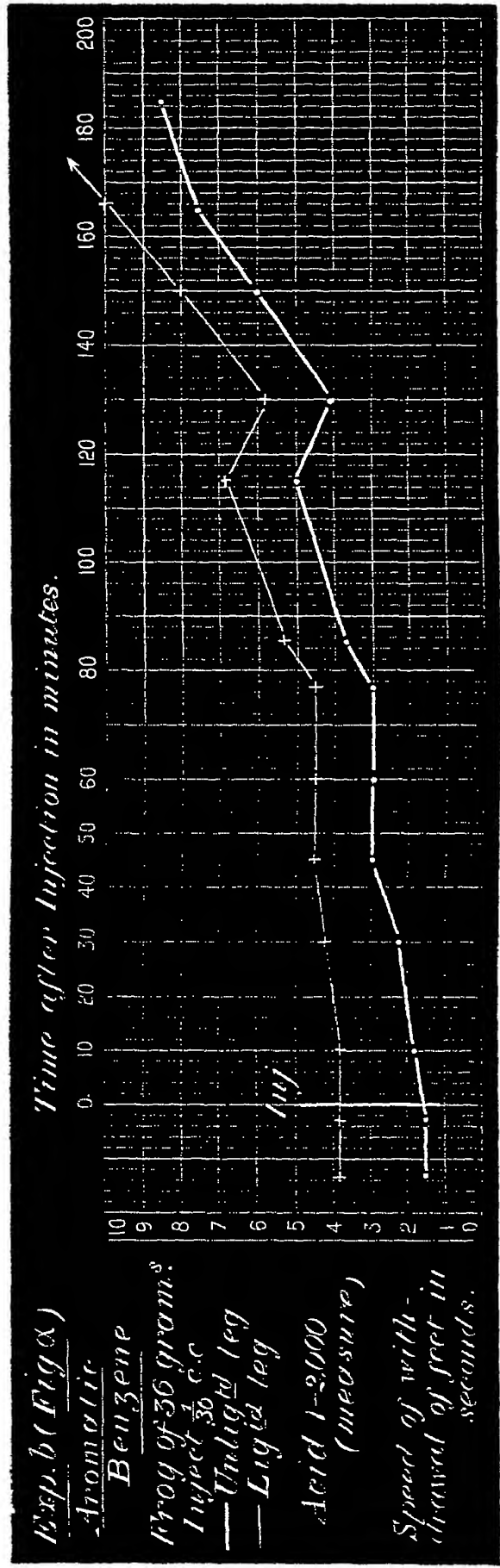
Time	Unligatured leg	Ligatured leg	Remarks
minutes	seconds	seconds	
0	1 5-2	2 5	
10	1 5	2	
20	3	3 5	Jerking of feet and spreading of toes commenced
40	10	9	Change to 1-2000 acid
50	2 5	2 5	Jerking exaggerated on instant of immersion
60	3	3-3 5	
120	6-6 5	6 5	Legs jerked out sharply, but thrust in again, the movement is exaggerated for some time after falling in water
180	8 9	8 9	
In 24 hours the reflex of this Frog was good, and but slightly tremulous			

*Experiment b* (Fig 12, a)

FROG of 36 grms. Preparation as before

Time	Unligatured leg	Ligatured leg	Remarks
minutes	seconds	seconds	
0	1 5	3 5-4	Tested four times at short intervals Acid solution 1-2000
Injected $\frac{1}{36}$ c c aromatic benzene			
10	1 5-2	3 5-4	
30	2-2 5	4-4 5	
45	3	4 5	
60	3	4 5	Withdrawal tremulous
85	3 5-4	5-5 5	
115	5	6 5-7	All movements are flapping and unsustained
130	4	5 5-6	
150	6	8	
166	7-8	10	
190	8 5	Not in 20	Next day reflex from both legs was good to mechanical stimulation

Fig 12





*Monochlorobenzene*

This compound causes a powerful effect upon reflex, it is, in fact, one of the most active bodies in the series. In about one-half of the experiments a shortening of the reflex period was produced immediately after injection. The reduction varied from 5 second to 1.5 second, and was never present for more than 30 minutes after the injection had been made. After this temporary reduction, or an alternative equality or slight lengthening of reflex, a very rapid change took place, the period of reflex increasing considerably with every estimation. Spontaneous spreading of toes and jerking of feet and legs were developed in all cases, and this condition was increased by immersion in the acid solutions, and sometimes persisted for a time in exaggerated form after washing with cold water. Immersing suddenly in water caused an active instantaneous jerk. In several experiments the ligatured leg, though as much affected in this respect as the unligatured, was stronger in its reaction, and, spite of diminished irritability from stasis, came to respond by withdrawal more rapidly than the other, indicating a direct paralysing action of the drug on the side of free circulation.

*Experiment c (Fig. 13,  $\beta$ )*

FROG of 28 grms Usual Preparation

Time	Unligatured leg.	Ligatured leg.	Remarks
minutes 0	seconds 1-1 5	seconds 2	Acid 1-2000 (measure) Tested reflex four times at intervals
Injected $\frac{1}{18}$ c.c. monochlorobenzene into anterior lymph sac			
10	5-1	1 5-2	Twitching of toes has commenced
20	5-1	1 5-2	
30	2	3	
40	2 5-3	3	Twitching of toes and feet active
60	8	5	
24 hours. All reflex gone			

Fig 13,  $\beta$  and  $\gamma$ *Experiment d. (Fig. 13,  $\gamma$ )*

FROG of 46 grms Usual Preparation

Time	Unligatured leg	Ligatured leg	Remarks
minutes	seconds	seconds	
0	2-2.5	2.5	1-4000 acid Tested reflex thrice
	Injected $\frac{1}{36}$ c.c. monochlorobenzene into anterior lymph sac		
10	2-2.5	3	
20	2.5	3-3.5	
30	3	4-4.5	
50	4	6	Movement broken and tremulous
70	5	9	Active jerking before withdrawal
90	13	Not out in 20 secs	

On changing the solution to 1-1000 (nothing weaker caused withdrawal), the reflex of the unligatured limb was reduced to 5 seconds, but lengthened again with moderate rapidity to 10 seconds. The ligatured limb yielded no further response. In 24 hours there was feeble reflex on the unligatured side, and in 48 hours this had become moderately active.

*Monobromobenzene.*

The action of this body upon reflex is considerable and moderately rapid, though it is distinctly less than that of monochlorobenzene. There is during the course of the experiment an almost entire absence of the motor phenomena which are so prominent in the former. No distinct reduction in the time of reflex was observed. The curves obtained from the ligatured and unligatured limbs ran fairly parallel. In the experiment quoted the latter at first was slightly slower than the former, but the position became in time reversed.

*Experiment e (Fig 14, δ)*

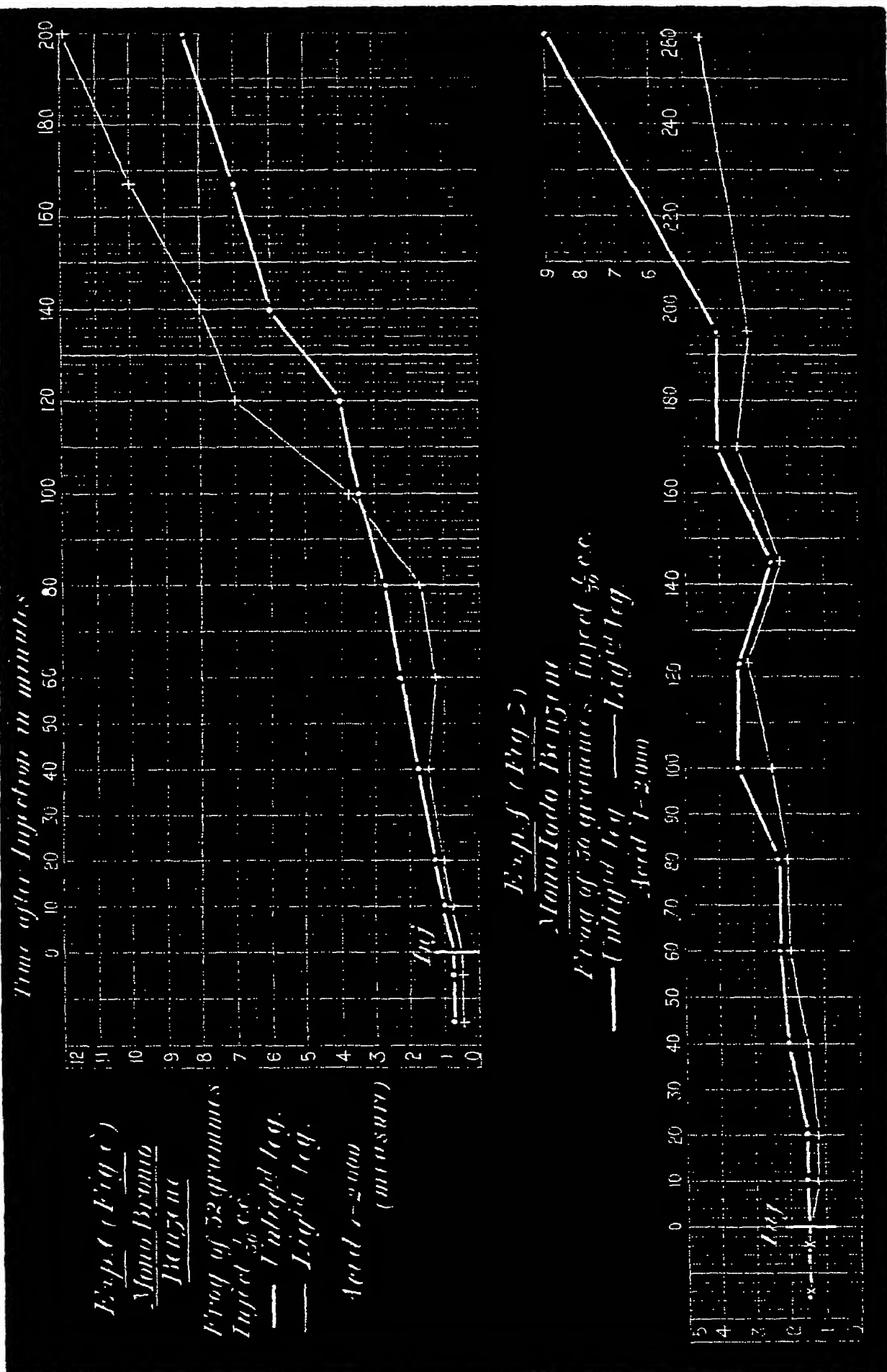
FROG of 32 grms Usual Preparation.

Time	Unligatured leg	Ligatured leg	Remarks
minutes	seconds	seconds	
0	5-1	5	Tested thrice at intervals    Acid, 1-2000
Injected $\frac{1}{8}$ c c monobromobenzene into anterior lymph sac			
10	1	5-1	Withdrawal tremulous, but no spontaneous jerking
20	1-1 5	1	
40	1 5-2	1 5	
60	2-2 5	1-1 5	
80	2 5-3	1 5-2	
100	2 5	3 5-4	
120	4	7	
140	6	8	
175	7	10	From 1-4000 acid solution
200	8 5	12	
275*	12	18	
24 hours    Reflex entirely disappeared to all stimulation			
* Not shown in fig			

*Moniodobenzene*

Of the haloid compounds, iodobenzene is the least active upon reflex. Although it does not appear to reduce the reflex period in the first instance, the prolongation caused as a rule develops slowly. In experiments extending to 4 and 5 hours it was found that the ligatured leg, at the conclusion, usually had a distinctly shorter reflex latency than its unligatured companion, from which circumstance a direct effect of the drug upon the terminal nervous filaments or the muscular tissue, impairing their function, is to be inferred. The spontaneous jerkings appear like those caused by chlorobenzene. A persistence of reflex on the day after the experiment appeared more usual than with the other haloid compounds for equal doses to animals of equal weight.

Fig 4 and



*Experiment f (Fig 14, e)*

FROG of 30 grms Usual Preparation

Time	Unligatured leg	Ligatured leg	Remarks
minutes 0	seconds 1 5	seconds 1-1 5	Tested thrice at intervals    Acid 1-2000
Injected $\frac{1}{36}$ c c moniodobenzene into anterior lymph sac			
10	1 5	1-1 5	
20	2	1-1 5	
40	2	1 5	
60	2-2 5	2	
80	.		Withdrawal becoming tremulous on both sides
100	3 5	2 5	
125		3-3 5	No spontaneous jerking
140	2 5	2-2 5	
170	4	3 5	
195	4	3	
260	9	4 5	
24 hours    Moderately good reflex in both legs			

The action of *methylbenzene* is apparently identical with that of the dimethyl compound, which we shall now consider.

*Dimethylbenzene.*

The effect produced by this compound upon the time of recovery is neither rapid nor powerful, and this statement holds even when the larger dose,  $\frac{1}{18}$  c c, is employed. A reduction of the latency has been observed in a considerable proportion of the experiments made with this drug, and this phenomenon has occasionally been seen to last for 40 minutes. Failing a positive reduction, the speed of withdrawal remains for a time unaffected. When the reflex does begin to lengthen the increase is gradual. There is no spontaneous movement. The reflex after the lapse of 24 hours is good and destitute of tremor.

*Experiment g* (Fig 15, ζ)

(The time of reflex was identical for a considerable period in the two legs)

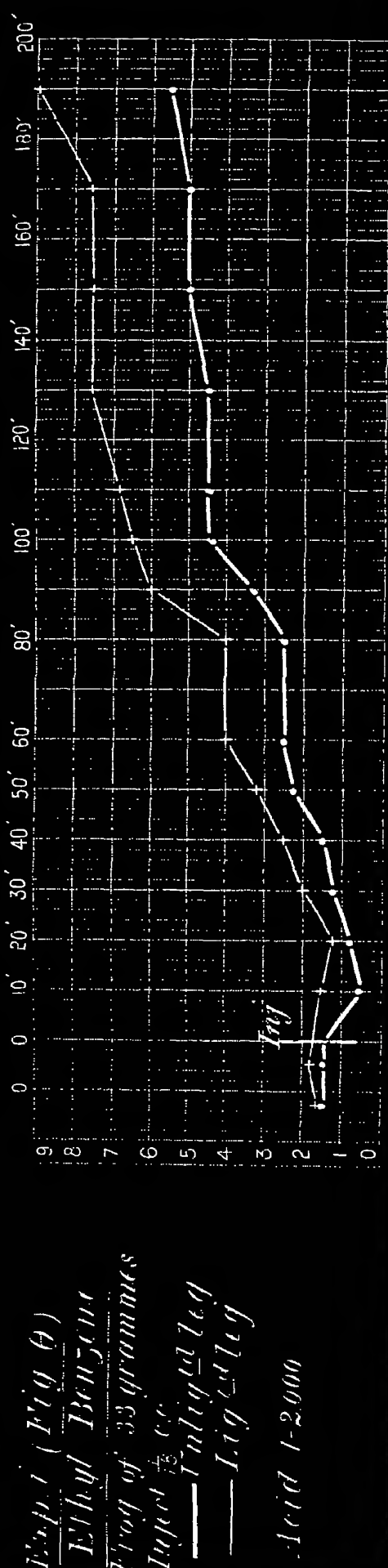
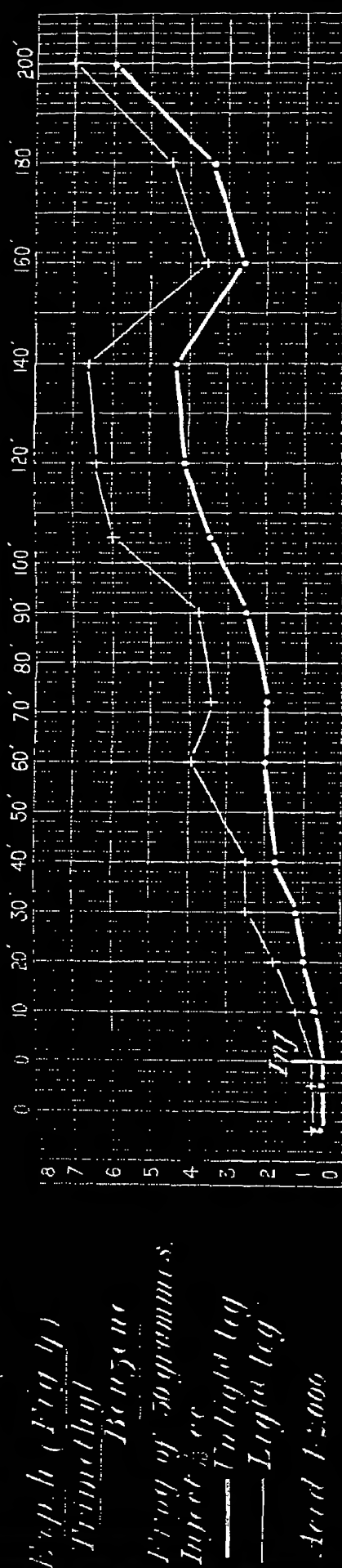
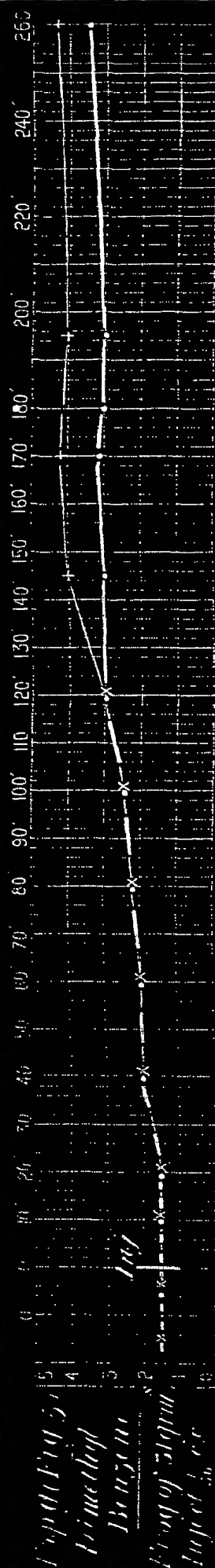
FROG of 31 grms Usual Preparation

Time	Unligatured leg	Ligatured leg	Remarks
minutes 0	seconds 1 5	seconds 1 5	Tested four times at intervals    Acid solution 1-2000
Injected $\frac{1}{86}$ c c dimethylbenzene into anterior lymph sac			
10	1 5	1 5	
20	1 5	1 5	
40	2	2	
60	2	2	
80	2-2 5	2-2 5	
100	2 5	2 5	
120	3	3	
145	3	4	
170	3-3 5	4-4 5	
195	3	4	
260	3 5	4 5	
24 hours. Reflex moderately good, devoid of tremor			

*Trimethylbenzene*

This compound is markedly stronger in its action upon reflex than the dimethyl compound. No shortening of reflex has been noticed, but a steady prolongation of the time elapsing between immersion and withdrawal of the foot. As a rule, the curves obtained from the ligatured and unligatured legs respectively run fairly parallel, but occasionally the unligatured drops behind the other, as if eventually a direct effect was produced upon the muscle substance and nerve terminations.

In 24 hours after the smaller dose reflex has, as a rule, entirely disappeared.

Fig 15,  $\zeta$ ,  $\eta$ , and  $\theta$ .



*Experiment h (Fig 15, η)*

FROG of 30 grms Usual Preparation

Time	Unligatured leg	Ligatured leg	Remarks
minutes	seconds	seconds	
0	5	5-1	Thrice tested at intervals    Acid solution 1-2000
Injected $\frac{1}{8}$ c c trimethylbenzene into anterior lymph sac			
10	5-1	1-1 5	
20	1	1 5-2	
30	1-1 5	2-3	
40	1 5-2	2 5	
60	2	4	
70	2	3 5	
90	2-3	3 5-4	
110	3-4	6	Well withdrawn    No tremor
130	4	6 5	
150	4-4 5	6 5-7	
170	2 5	3 5	A most distinct acceleration of reflex, regular on every immersion
190	3 5	4 5	
210	6	7	
24 hours    All vitality gone			

*Ethylbenzene.*

Although the effect produced upon reflex is moderately rapid and extensive when large doses have been administered, with smaller doses the result is much less marked, so that this compound is to be regarded as amongst the feeblest in its power of reducing the reflex activity of the cord. As a primary result of its action the time of reflex is usually reduced, sometimes by as much as 1 second. This stage of acceleration may persist from 10 to 30 minutes. Thereafter a lengthening of the period occurs and develops slowly or rapidly according to the dose. There is no protraction of spontaneous tremor and jerking, though the withdrawal of the legs becomes ultimately tremulous.

The day after the experiment, when the smaller dose had been used, the reflex was usually found to be good and unaccompanied by tremor.

*Experiment 1. (Fig 15, θ)*

FROG of 33 grms

Time	Unligatured leg	Ligatured leg	Remarks
minutes	seconds	seconds	
0	1.5	1.5-2	Tested four times    Acid 1-2000
Injected $\frac{1}{8}$ c.c ethylbenzene into anterior lymph sac			
10	1	1.5	
20	5-1	1	
30	1-1.5	2	
40	1.5	2.5	
50	2-2.5	3-3.5	
60	2.5	4	
70			
80			
90	3-3.5	6	
100	4.5	6.5	
110	4.5	6.5-7	
130	4.5	7.5	
150	5		
170			
190	5.5	8	

In Experiment k, in which a Frog of 38 grms received  $\frac{1}{8}$  c.c of ethylbenzene, the time of reflex, when tested with 1-2000 acid, increased in 140 seconds by less than 2 seconds, and in 2 hours later it had increased only one additional half second. The day after the preparation showed good reflex in both legs; no tremor was present.

*Anilobenzene.*

Anilin has considerable power in causing spontaneous movement in a pegged Frog. The movement is spontaneous, but it is exaggerated on dipping the foot into acid solution or even into water. No reduction of the reflex period has been observed. The time occupied in withdrawal lengthens materially, whilst the increased jerking immediately after immersion shows it is a case of slow summation of stimulations centrally rather than of a failure of peripheral motor and sensory apparatus. The curves of response of the ligatured and unligatured legs are very parallel throughout.

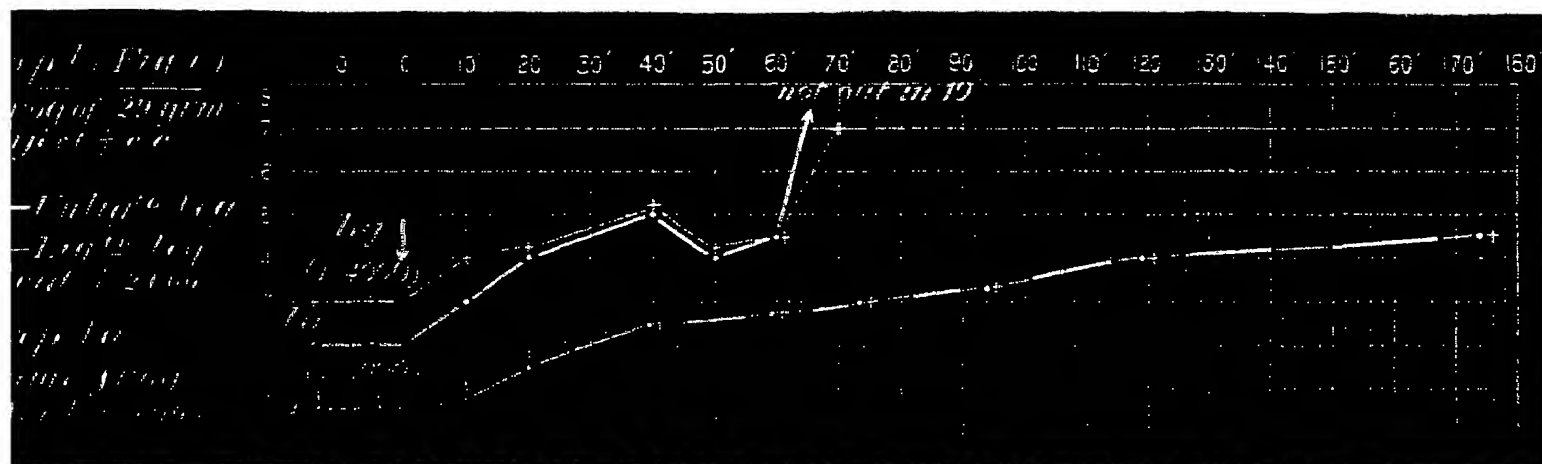
If the acid solution used is of the strength of 1-2000, and the amount of anilin injected does not exceed  $\frac{1}{8}$  c.c., reflex may still occur within three or four seconds of the original speed, even after the lapse of three hours.

*Experiment 1, la (Fig 16 v)*

FROG of 29 gms Usual Preparation

Time	Unligatured leg	Ligatured leg	Remarks
minutes	seconds	seconds	
0	5	5-1	Thrice repeated at intervals Acid 1-2000
			Injected $\frac{1}{15}$ c c amidobenzene
10	5-1	1	Withdrawal tremulous
20	1 5	1 5-2	
40	2	2	Twitching of toes increased even after acid removed by washing
50	2 5	2 5	
60	2 5-3	2 5-3	
75	3	3	Are only just drawn clear of the solution The ligatured leg is the stronger of the two
95	3-3 5	3-3 5	
120	4	4	Withdrawal very weak and tremulous Jerking and spreading of toes after washing
175	4 5	4 5	
Same preparation tested at same time with 1-4000 acid solution			
0	2	3	
Time of injection			
10	3	4	
20	4	4-4 5	
40	5	5-5 5	
50	4	4-4 5	
60	4 5	4 5	
70	Not out in 10	7	

Fig 16 v



*Nitrobenzene*

Little or no movement of the reflex frog preparation is observed independently of the stimulation

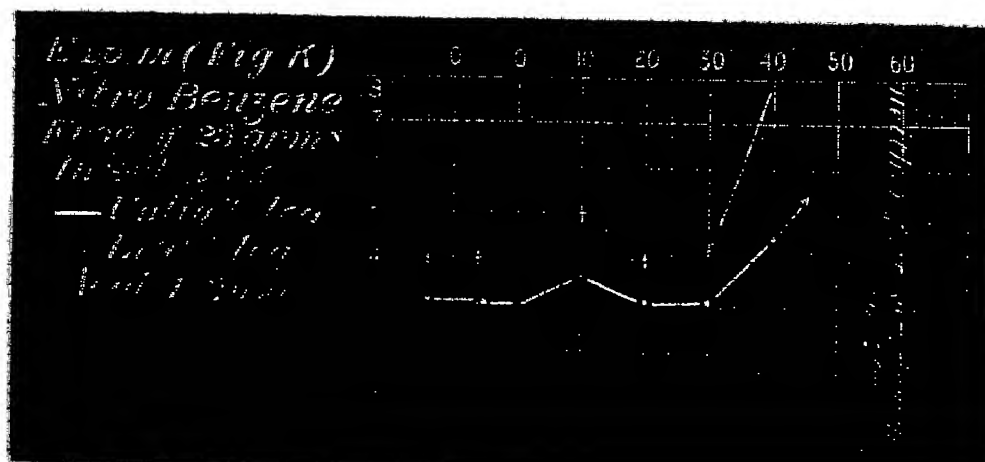
If the dose of nitrobenzene injected is a moderately large one ( $\frac{1}{18}$  c c to frog of 23 grms), great prolongation of reflex is observed usually within an hour. Thus, in the case referred to, in 60 seconds after injection neither leg was removed within 20 seconds, though at 20 minutes the reflex stood at 3 seconds and 4 seconds for the two legs respectively. A dose proportionately much smaller, as in the case quoted ( $\frac{1}{36}$  c c to frog of 41 grms.), shows a comparatively slight effect upon the cord, the reflex remaining active, with but little tremor on stimulation. After the smaller dose recovery frequently takes place, so far that reflex next day is good on the side of ligature, and the withdrawal of the protected foot occurs more powerfully on stimulating the unprotected than the withdrawal of the latter itself. It is evident, therefore, that sensory nerves are no more affected than motor, if as much, by the action of this drug, which has a direct effect upon the exposed limb in addition to its action on the cord.

*Experiment m. (Fig. 17, κ.)*

FROG of 23 grms. Usual Preparation

Time	Unligatured leg	Ligatured leg	Remarks
minutes	seconds	seconds	
0	3	4	Tested thrice Acid 1-2000
			Injected $\frac{1}{18}$ c c nitrobenzene
10	3.5-4	5	
20	3	4	
30	3	4.5	
40	4.5	8	
60	Neither out in 20		

Fig 17, κ.



*Experiment n*FROG of 41 gms    Injected  $\frac{1}{36}$  c c Nitrobenzene

In this experiment reflex on immersion in 1-4000 acid solution became gradually slower, but after 3<sup>1</sup> the ligatured leg was still withdrawn in 4<sup>s</sup> (instead of 1<sup>s</sup> before injection) and the ligatured in 5<sup>s</sup> (instead of 1<sup>5</sup>s)

When a reflex Frog poisoned with nitrobenzene is laid on a flat surface, the legs, if flexed, are not violently extended with jerking and tremor, as in the case of monochlorobenzene, amidobenzene, &c, but are retained in a flexed position.

## SECTION III—THE ACTION OF BENZENE COMPOUNDS IN CAUSING MUSCULAR RIGOR

It had been frequently observed that local coagulation of muscle was produced at parts with which the benzene compounds had come into contact, it seemed advisable therefore to determine whether the activity of these bodies was uniform or whether some were more active than others. With this object in view the compounds were either brought into direct contact with the muscle by filling the muscle chamber already described ('Phil Trans,' Part I, 1884) with them, so that the muscle was completely immersed, or else measured quantities were introduced into a muscle chamber which was specially constructed so as to be absolutely air-tight, and thus without bringing the liquid into direct contact to allow of its action during volatilisation upon the muscle.

By the first method it was found that powerful rigor was rapidly induced by all the members of our series. The contrast between the three halogen compounds showed that in the case of—

Monochlorobenzene, the active shortening of the muscle		
30 minutes after application of the drug was	. . .	3.1 millims
Moniodobenzene, the active shortening of the muscle		
30 minutes after application of the drug was	. . .	3.4 „
Monobromobenzene, the active shortening of the muscle		
30 minutes after application of the drug was	. . .	2.5 „

In each case contraction commenced within one minute of contact with the benzene compound.

As this method however involved the use of such large quantities of the compounds the series was not completed, but the second plan (*i.e.*, the spontaneous volatilisation of carefully measured amounts of the compounds in an air-tight chamber, into which a muscle had previously been introduced) was followed.

The contrast was made at equal temperatures.

By following this plan it was soon determined that variations occurred between the various benzenes. Shortening of the muscle did not immediately occur as in the case of immersion which has been already described. It was even found that when stimulation of the muscle was practised before and after the admission of the benzene compound, the contraction occasionally remained as powerful for some time under the latter conditions as it was before, but this was always in absence of any material shortening. The variation between the bodies with regard to this as well as to the shortening was, however, considerable. Some proved themselves distinctly more active than others.

When  $\frac{1}{10}$  c.c., exactly measured, of the *halogen* compounds was introduced, it was found that monochlorobenzene was much the most active in causing rigor, then monobromobenzene, and monoiodobenzene was a good deal weaker than either of them.

When the strongest of these bodies (monochlorobenzene) was contrasted with the alkyl compounds it was found to take an intermediate place between methyl-, which is the strongest, and dimethylbenzene which stands next to it; when contrasted with the third of the methyl compounds, trimethylbenzene, monochlorobenzene shows itself itself later in producing shortening, but its ultimate effect is more powerful.

The activity of the methyl compounds is therefore inversely to the extent of methyl substitution in the benzene molecule.

Ethylbenzene is not far removed from methylbenzene in the total effect of the shortening it produces. In each of four experiments the latter was strongest. It is generally quicker in causing shortening than methylbenzene. Ethylbenzene is distinctly stronger than the di- and trimethyl compounds.

With such small quantities as  $\frac{1}{30}$  c.c. of these compounds a very distinct and moderately rapid shortening was induced, as the following figures, illustrative of a few experiments only, suffice to show, the contrast in each instance being between companion muscles of the same Frog at equal temperatures. Two slow drums were employed, having a slightly different speed of rotation.

No. 1 has a rate of 33 millims. in 10 minutes. Figs. 18 and 19.

No. 2        „        39        „        „        „        Fig 20.

Nitrobenzene and amidobenzene showed themselves much less effective than the other compounds when muscles were exposed in air-tight chambers to their action.

In experiments in which only the  $\frac{1}{30}$  c.c. of these bodies was tested, it was found that after the lapse of 15 hours no shortening nor rigor were observable.

When the muscles were exposed for many hours in the presence of a large amount of these bodies, mononitrobenzene was earlier in producing its effect than anilin.

# COMPARATIVE ACTION ON MUSCLE—Rigor

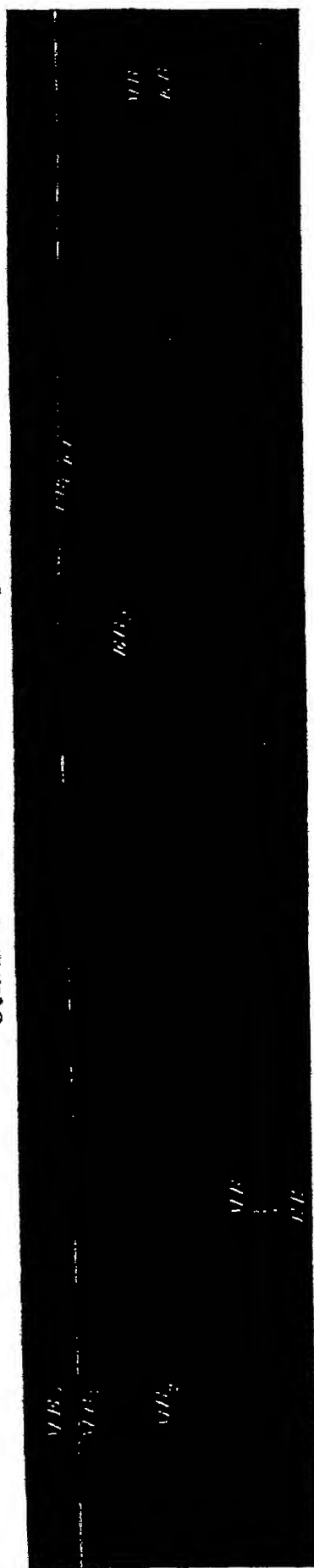


Fig 18 Ethylbenzene and Methylbenzene



Fig. 19 Methylbenzene and dimethylbenzene

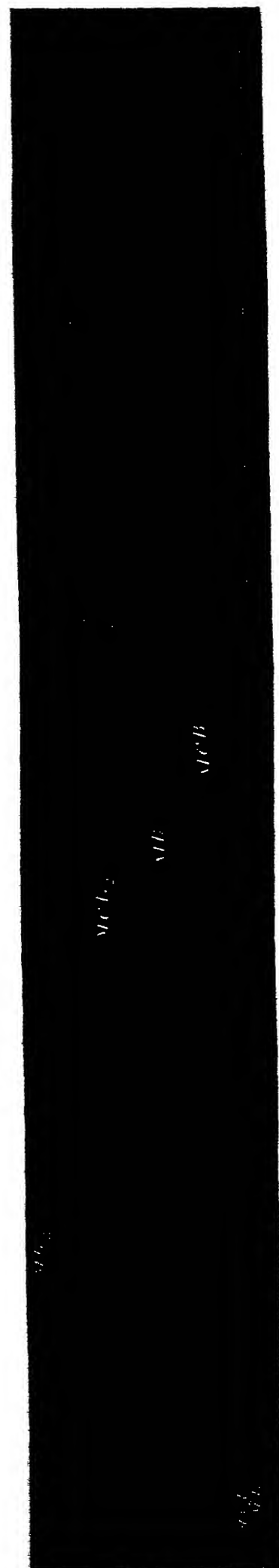


Fig. 20 Monochlorobenzene and methylbenzene



Substance	Amount	Temperature in °C	Frog's muscle	Weight	Time of first sign of contraction.	Contraction			
						Extent 30 minutes after exposure	60 minutes	2 hours 4 minutes	12 hours
	cc	°		grams	min sec	millims	millims	millims	
Monochlorobenzene } fig 20	1/30	12 75	Triceps	10	15 0	15	3		
Methylbenzene	"	"			7 10	25	42		
Methylbenzene . } fig 19	"	10	Gastrocnemius	10	6 0	41			
Dimethylbenzene	"	"	"		8 12	23			
Methylbenzene . }	"	12	Gastrocnemius	10	10 0	26	53		
Trimethylbenzene	"	"	"	"	13 0	8	53		
Methylbenzene } fig 18	"	11 75	Gastrocnemius	10	6 30	27	61	7	
Ethylbenzene	"	11 75	"		9 45	25	56	65	
Ethylbenzene }	"	11 25	Triceps	10	9 20	43	73		
Trimethylbenzene	"	"			13 20	13	43	67	
Amidobenzene . }	"	12	Triceps	10	Not in 14 hours				
Nitrobenzene . }	"	"	"	"	"				Not in 14 hours

This result would not seem to point away from the theory which might possibly be advanced, that we have here to do to a large extent with a question of varying volatility between the various benzenes.

The boiling-points of amidobenzene and nitrobenzene are 184 and 209 respectively, and the only body which at all approaches them in the slowness of its action is moniodobenzene, with a boiling-point of 188

Ethylbenzene, with a boiling-point of 134, comes after methylbenzene (111), but before dimethyl- (146) and trimethylbenzene (163)

#### SECTION IV—EXPERIMENTS UPON RATS

Benzene, and the compounds of the benzene series, together with resorcin, were administered hypodermically to Rats, the animals chosen for experiment being as nearly as possible of the same size

##### *Aromatic Benzene*

Produces lethargy, with some exaggeration, however, of reflex, and occasional spontaneous jerking, with great impairment of mobility

##### *Experiment*

Injected 5 gtt into right groin

- 19<sup>m</sup> Is torpid, but can run easily if roused.
  - 31<sup>m</sup> Is hyperæsthetic and jerks away, if touched, to another place
  - 36<sup>m</sup> Starts if touched There is an occasional spontaneous jerk
  - 60<sup>m</sup> Much less affected than either of the others (nitro- and amidobenzene) examined at the same time
  - 80<sup>m</sup> Falls over on one side if touched
  - 260<sup>m</sup> Sitting up and beginning to run
  - 300<sup>m</sup> Normal
- Next day perfectly normal

Small doses of monochloro-, monobromo- and moniodobenzene (2 minims) injected beneath skin of three Rats of equal medium size, caused in each case slight lethargy without any special symptoms. This lethargy continued for from 60 minutes to 90 minutes, after which time complete recovery occurred.

##### *Larger Doses.*

*Chlorobenzene.*—6 minims injected beneath skin caused some tremulousness in movements in 30 minutes. The animal became lethargic, and if not roused remained sitting in corner of cage. It was, however, easily roused by touching or noise, and then ran well, though its movements were somewhat unsteady. This condition lasted

for three hours after administration of chlorobenzene, and thereafter a return to normal took place

*Bromobenzene*.—After a similar dose of this drug a Rat of equal size became very lethargic, and though sitting up and possessed of all its reflexes, it could hardly be roused to movement

When recovering it walked slowly with a rolling or rocking movement, its balance appearing uncertain

*Iodobenzene*.—Was distinctly more active than either of the other haloid compounds (6 minims to animal of equal size to other two)

- 12<sup>m</sup> After administration it was observed to jerk five or six times in succession, became rapidly weak tending to sink on its side
- 27<sup>m</sup> Resting on side Very lethargic All reflexes are present
- 37<sup>m</sup> Breathing much accelerated Rocks as if attempting movement, but lies in any position in which it is placed.
- 2<sup>h</sup> 42<sup>m</sup> Symptoms are more marked than at the last report The animal cannot move trunk or limbs The eye reflex still persists No tremor Breathing rapid
- The conditions remained much the same till death occurred in 5 hours from failure of respiration
- Post-mortem Right heart contains much dark blood No other special appearances

Subcutaneous injection of 6 minims of ethyl-, methyl-, and dimethylbenzene respectively, caused a condition of lethargy which lasted from three to four hours The animal could be roused at any time No special motor symptoms were produced, but a certain degree of anæsthesia was observable in each instance.

Trimethylbenzene of the same dose caused closely similar symptoms, but terminating in the death of the animal

### *Dioxybenzol on Rats*

0.03 gm. of metadioxybenzol, dissolved in five drops of salt solution, injected subcutaneously into large Rat

- 3<sup>m</sup>. Shuddering and jerking of body, shaking of head
- 9<sup>m</sup>. Above symptoms much more marked
- 12<sup>m</sup>. Still walks, but very ataxic Breathing accelerated
- 18<sup>m</sup> Resting on side and back, cannot rise, all limbs in clonic spasm Abdominal, thoracic, cervical, and facial muscles also contract sharply at intervals No fixed or tonic spasm
- 41<sup>m</sup> This condition continued until 41<sup>m</sup> after the injection, when jerking became less, and the power of spontaneous movement began to return. Washed face and walked a few paces
- 51<sup>m</sup>. Reflex is still rather exaggerated, but spontaneous jerking has almost disappeared
- 80<sup>m</sup> Quite normal

Doses of 0.05 to 0.1 were fatal; death occurred from paralysis of the respiratory muscles. The heart appeared to be relatively not much affected, its action outlasting the respiration.

(Pyrogallie acid was not examined in this series.)

*Amidobenzene on Rats*

Rapidly developing weakness, with jerking and marked dyspnœa, is observed

- Injected 4 minims into right groin
- 15<sup>m</sup> Tends to sink on belly Hind legs weaker than fore
- 18<sup>m</sup> Breathing over 200 per minute An occasional start or jerk is noticed Can still crawl very slowly, but usually lies with legs extended behind it
- 57<sup>m</sup> Is much more affected than the benzene or nitrobenzene Rats
- 87<sup>m</sup> A good deal of jerking as it lies, both of fore and hind limbs Much dyspnœa
- 107<sup>m</sup> Breathing very hurried great dyspnœa
- 262<sup>m</sup> Quite insensible; no reflexes Jerking of limbs at intervals, as 2<sup>s</sup>, 5<sup>s</sup>, 5<sup>s</sup>, 3<sup>s</sup>, 2<sup>s</sup>, &c Respiration rapid and laboured, 150 per minute Body not very cold Breath smells of amidobenzene
- 342<sup>m</sup> Died
- Only very slight twitch of toes occurred on crimping sciatic
- Post-mortem—Limp, cortex of kidneys and brain surface congested Right side of heart very full

*Nitrobenzene on Rats*

Torpidity, weakness, failure of reflex, absence of motor symptoms. Failure of respiration

- Injected 5 minims into right groin
- 38<sup>m</sup> Runs, but is weaker and somewhat torpid
- 53<sup>m</sup> Runs a step or two and falls on side, but soon recovers itself
- 83<sup>m</sup> Rises with difficulty if turned over on side
- 130<sup>m</sup> No marked reflex from body or limbs, but from eye still present Breathing quiet, not hurried
- 258<sup>m</sup> More under influence of drug Is now profoundly insensible to all stimulation Breathing and pulse feeble Surface very cold.
- 358<sup>m</sup> Breathing slower, no twitching, no reflex, quite insensible
- 500<sup>m</sup> Died
- Post-mortem—Lungs congested Right heart contracted, also left Kidneys not markedly hyperæmic (in these respects differs from amidobenzene)

## SECTION V ACTION OF AROMATIC BENZENE AND ITS COMPOUNDS ON PULSE, BLOOD-PRESSURE, AND RESPIRATION OF MAMMALS.

In all cases ether was the anæsthetic employed during the experiments This was administered from a bottle which was connected with the tracheal cannula by means of a short tube By turning the stop-cock (Dr BRUNTON'S\*) with which the bottle was provided, atmospheric air was substituted for ether. The animal was kept thoroughly anæsthetised, but never profoundly narcotised.

*Aromatic Benzene.*

Experiments made with this substance yielded fairly similar results.

The blood-pressure was for some time but little affected (in one instance slightly increased), and the character of the pulse was not materially altered, although it was considerably reduced in frequency.

The respiration showed at first a slight acceleration, but this soon yielded to a

\* 'Brit Med. Journal'

marked slowing, with a slowly developing and relatively prolonged inspiratory phase. The heart became irregular, with incomplete diastole.

As the amount of the drug injected was increased, the respiratory waves became more marked in the blood-pressure curve.

Section of the vagi caused a distinct rise of blood-pressure and an acceleration of the pulse. The respiration was reduced to about one-half of its previous frequency. In the experiment which we shall now quote, death took place suddenly after injection of benzene into the intestine. Both vagi had been previously divided, and death was due to cardiac arrest.

CAT of 6 lbs weight Etherised Cannulae in Trachea and Right Carotid Arteries.

Both Vagi prepared Loose on Threads. Animal placed in Warm Box Arrangement of Apparatus as usual

Time	Remarks	Pulse for 1 minute	Blood-pressure	Respiration
minutes				
10				
18	10 minims benzene injected subcutaneously	110	120	21
38		112	132	26
43	20 minims benzene injected subcutaneously			
60		143	110	15
70	Respiratory waves of blood pressure very extensive, causing variation of 9 millims	..	111	
75	20 minims benzene			
93	" "			
115		108	126	18
120	Inject 30 minims as before			
155	" "			
165	Systole incomplete Fluctuations owing to respiration irregular Groups of two or three hurried cardiac contractions may be followed by a somewhat longer diastole			
175	Ligature of left vagus causes rise of 22 millims, which persists for few seconds, then a return to previous level			
192	Ligature of right vagus causes temporary rise of 19 millims, and a more permanent rise of 5 millims			
194		132	118	9
205	Stimulation of peripheral end causes fall of 20 millims			
210	Shows great irregularity.		120	
215	Opened abdominal cavity, exposed loop of intestine		132	
230	Injected 10 minims benzene into loop of intestine	..	120	
233	Rapid fall of pressure, heart having stopped Attempts at respiration continued 3 <sup>m</sup> after heart had ceased			

*Post-mortem.*—The right auricle and ventricle were dilated and full of dark blood. Left ventricle firmly contracted. Lungs slightly congested, but otherwise not abnormal.

Intestine very full of flatus; irritable. Stimulation of sciatic nerve gave firm tetanus of gastrocnemius.

*Monochlorobenzene.*

When injected subcutaneously in an emulsified condition, monochlorobenzene was found at first to raise the blood-pressure and to accelerate the pulse and respiration. The blood-pressure remained high throughout the first two hours, during which time one drachm had been injected (in experiment quoted below). The pulse rate was also increased. Some slowing of the respiration was produced eventually. Whilst large doses injected subcutaneously did not produce more marked action, small doses, in a fine state of emulsion, injected into the femoral vein caused cardiac arrest, respiratory efforts outlasting the heart's action.

After the injection of this drug, ether appeared in one case to have an unusually depressant action on the heart.

MONOCHLOROBENZENE Cat 5 lbs Etherised. Cannulae in Trachea and Femoral Vein  
Animal in Warm Box

Time	Remarks	Pulse for 1 minute	Blood- pressure	Respiration
minutes 0-20		123	134-162	25
20	Injected 20 minims monochlorobenzene (emul- sionised) subcutaneously			
38	. . . . .	132	165	30
60	. . . . .	..	181	
67	Injected 20 minims monochlorobenzene			
77	If anaesthesia is not profound there is con- siderable tremor of limbs			
85	On giving ether, first a fall, then rise, then rapid fall of blood-pressure to 9 millims Division of both vagi and artificial respiration caused recovery			
105	.	168	156	22
120	Injected 20 minims as before			
125	" " "			
140	Clot formed in right carotid which could not be removed. Changed cannula to left carotid. Unusual tendency to clotting throughout the experiment			
158	Pulse somewhat dicrotic	164	124	22
172	.	..	116	
173	Injected 20 drops (emulsified) into femoral vein			
178	Heart ceased		0	
183	Respiratory effort ceased			

*Post-mortem*—Heart. Auricular appendix beating actively. Right ventricle in diastole, smelling strongly of monochlorobenzene. Left ventricle in strong systole. Lungs healthy, contain much mucus, but do not, on naked eye examination, show hæmorrhages or infarction. Gastrocnemius contracts well both to direct and indirect stimulation.

*Monobromobenzene*

Like aromatic benzene and monochlorobenzene this substance (monobromobenzene) was found to act very feebly when injected subcutaneously. Administered in this way some increase of blood-pressure with acceleration of the pulse was produced.

When injected into the jugular vein, very largely diluted, a small dose of 1 to 4 minims caused a slight rise of pressure if the injection was slow, but a fall if it was rapid. The respiration became greatly accelerated, sometimes irregular and gasping. When the pure drug was slowly injected without dilution, gasping respirations succeeded and ultimately complete paralysis of respiration. Even when the pure drug was employed very large doses were injected before death took place. Death was due, in the experiments made, to failure of the heart.

CAT of 8 lbs Preparation as usual Injection was made into the Jugular Vein

Time	Remarks.	Pulse for 1 minute	Blood pressure	Respiration
minutes				
0	(Fig. 21)	144	114	24
25	Injected 1 minim of monobromobenzene, thoroughly emulsified into the jugular vein			
60		148	111-115	
83	Injected 1 minim as before, but more rapidly. There is a fall of 18 millims. for a few seconds followed by rise of 4 millims.			
90	Injected 2 minims, shaken up in 3 c.c. salt solution, slowly. Rise of 3 millims., but if injection was made more rapidly there was at once a fall.		118	
92	Systole well maintained	126	110	46
105	Injected 4 drops as before, with a fall of pressure succeeded by a rise (fig. 22). Respiratory curves in blood pressure increased in extent.			
120	(Fig. 23).	144	94	44, rather irregular
130	Injected very slowly 8 drops (Injection occupied 9 minutes)	..	104	
140	(Fig. 24)	.	82-92	
150	Slow injection of 20 minims in 30 c.c. salt solution yields faint rise of pressure succeeded by gasping			
155		140	100	
162		.	110	0
165	Injection of 45 minims unsuspended into vein. Succeeded by salt solution. Respiration occasional and gasping. Pause in expiration.			
175-190	120 minims undiluted in all, injected in 3 doses.		100-32	
195	After first dose of 30 minims (fig. 25). Blood pressure falling, vagi are cut. Rise of pressure for few seconds, and the heart ceases.	131	43	5-6

*Post-mortem.*—Lungs engorged. Some ecchymosis observed on section. Left heart simply contracted. Heart dilated. Blood smells much of monobromobenzene. Kidneys congested, but showed no

*Intestines* exhibit peristalsis.



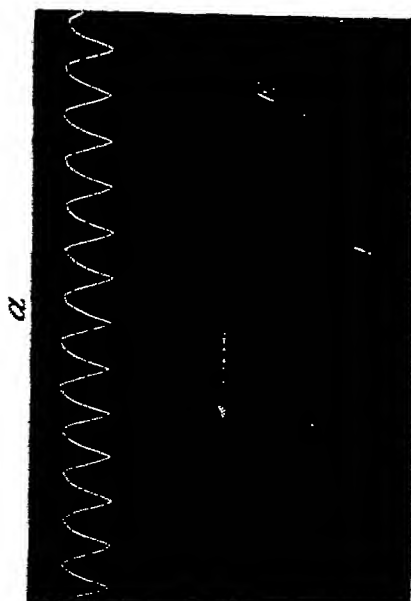


Fig. 21 Quick drum (55 millims. equal to 5\*) Pulse and respiration Before injection of monobromobenzene

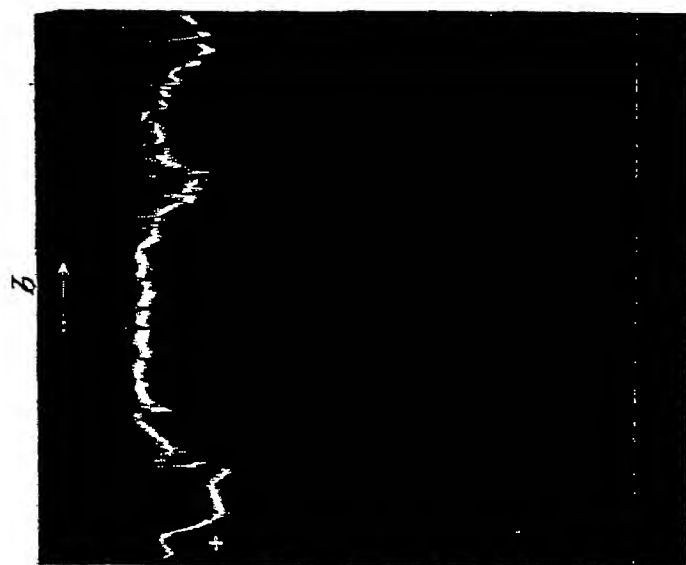


Fig 22 Slow drum (19.4 millims equal 5<sup>m</sup> in all experiments) \* Intravenous injection of 4 minims monobromobenzene. Time 105<sup>m</sup>

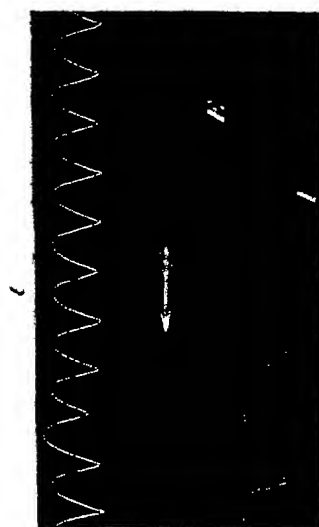


Fig 23 Quick drum Pulse and respiration Time 120<sup>m</sup>



Fig 24. Quick drum. Pulse and respiration 140<sup>m</sup>

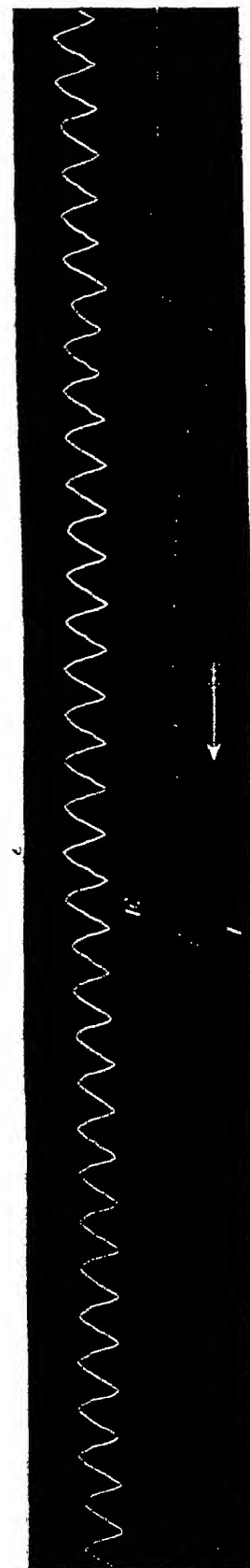


Fig 25. Quick Drum Pulse and respiration 180<sup>m</sup>

*Iodobenzene*

In the experiment which we shall quote, iodobenzene was injected into a loop of intestine which was carefully returned to the peritoneal cavity after the operation the small abdominal incision being closed

A slight increase of respiration was soon followed by a fall in the rate per minute

The heart was greatly accelerated, the increase in number of pulsations amounting to over sixty per minute. The blood-pressure which had remained fairly constant for two hours, rose considerably at the commencement of the third hour. After ligation of the vagi the pulse became even more rapid and the pressure higher. There was not, however, a very marked slowing of respiration. Death as usual was due to cardiac failure.

In the experiment quoted, death of the animal occurred suddenly after dilute ether vapour had been re-administered for a short time; the respiration outlasted the cardiac contraction. This result, or, short of it, a great and sudden fall in the blood-pressure, we have seen produced on several occasions by ether, when administered after large doses of the drugs contained in our series, even when the previous administration had been altogether unattended by any unusual effect of this character.

Cat, 8 lbs. Cannulae in Carotid and Trachea. Vagi prepared on loose threads.

Time	Remarks	Pulse for 1 minute	Blood-pressure	Respiration
minutes				
0	(Fig. 26)	132	110	25
22	Injected 5 minims moniodobenzene into a loop of intestines. Rise of 4 millims at time of injection, and more permanent elevation of 2 millims			
32		204	108	26
70	Injected 15 minims as before			
90	(Fig. 27)			
105	Injected 20 minims as before	180	110	20
160	" 30 "			
185	(Fig. 28)	204	124	25
140	Injected 30 minims as before			
210	Respiration feeble.	--	140	
212	Tied left vagus. Rise of 24 millims., then fall, first gradual then rapid, to 48. After which gradual recovery occurred. Ligatured right vagus	240	150	20
225	(Fig. 29)			
230	Administered ether. Blood-pressure fell to within 24 millims of abscissa, and in spite of artificial respiration being carried on in addition to spontaneous respiration, the heart did not recover itself			

## Tracings of the pulse by Fick's Kymograph Action of Moniodobenzene



Fig 26 Time 0 Pulse before injection of moniodobenzene

Fig 27 68<sup>m</sup> after first injection and after 20 *minims* in all of moniodobenzene have been injectedFig 28 163<sup>m</sup> after first injection and after 70 *minims* in all have been injectedFig. 29. 203<sup>m</sup> after the first injection Both vagi have been divided.*Methylbenzene (Toluene)*

When injected subcutaneously this substance causes a rise of blood-pressure, succeeded by a fall. The pulse is greatly accelerated. In the first instance the respiration is somewhat accelerated.

Intravenous injection accelerates the respiration at the same time that it reduces the blood-pressure and lessens the pulse-rate, the beats becoming irregular and fused without a complete diastole intervening. This depression of the blood-pressure is to some extent central, as there is a great rise after vagotomy, and the pulse becomes very rapid. The respiration was not so greatly slowed by this operation as is usually the case.

In the experiment we shall quote, death appeared to be due to pulmonary cedema.

CAT,  $7\frac{1}{2}$  lbs.

Time	Remarks	Pulse for 1 minute	Blood-pressure	Respiration
minutes				
0		118	122	26
12	Injected 12 minims methylbenzene subcutaneously			
25	Fluctuations appear in the blood-pressure tracing which are not of respiratory origin	164	134	
30	Ether abolishes these			28
45	Injected 20 minims subcutaneously			
60			120	
55	Waves now reappear	156	112	
78	Injected 2 minims in 2 c c salt solution into femoral vein. Waves become more marked; they are abolished by ether, which lowers blood-pressure			
85	Injected 5 minims in 10 c c salt solution At once a rise of 7 millims., succeeded by waves fluctuating from 94 to 108. (Fig. 30)			
92	These waves are abolished by ether			
100	Injected 8 minims as before	..	110	
103	Irregularity in pulse beats, which tend to form pairs without complete diastole intervening			
113	Irregularity of pulse disappeared Well sustained double summit, second somewhat lower than the first	119	99	40
115	Injected 8 minims as before		98	
117	Pulse irregular, with abortive systole preceding strong contraction of ventricle Cut vagi, pulse and pressure rise. (Fig. 31)			
120		144	114	21
128	Injected 10 minims rapidly	168	44	18
132		136	72	8
135			58	
138	About 20 c c of bloody serous fluid has come from cannula in last ten minutes Animal died of suffocation			

*Post-mortem.*—Both sides of heart (contain blood) in diastole. Right enormously distended Lungs very oedematous throughout, rosy red.

### *Dimethylbenzene (Para).*

When injected into a loop of the intestine which was then returned to the peritoneal cavity, dimethylbenzene somewhat lowered the blood-pressure and slowed both respiration and pulse in the first instance, subsequently the respiration became more rapid, the pulse nearly as rapid as it had previously been.

Small doses, 2 minims (largely diluted) injected into vein caused a transitory rise of pressure. Larger doses of 4 to 8 minims, also largely diluted, caused at once a fall succeeded by a slow return of the pressure to the former level.

Failure of respiration tended to occur. After vagotomy in the experiment recorded, the pulse became much accelerated, the pressure rose, and the respirations fell from

## Methylbenzene

Fig. 30. 117<sup>m</sup>. Division of vagi whilst inhibition from the drug was present. The tracing reads from right to left in the direction of the arrow, and 29 millims correspond to 5<sup>s</sup>.

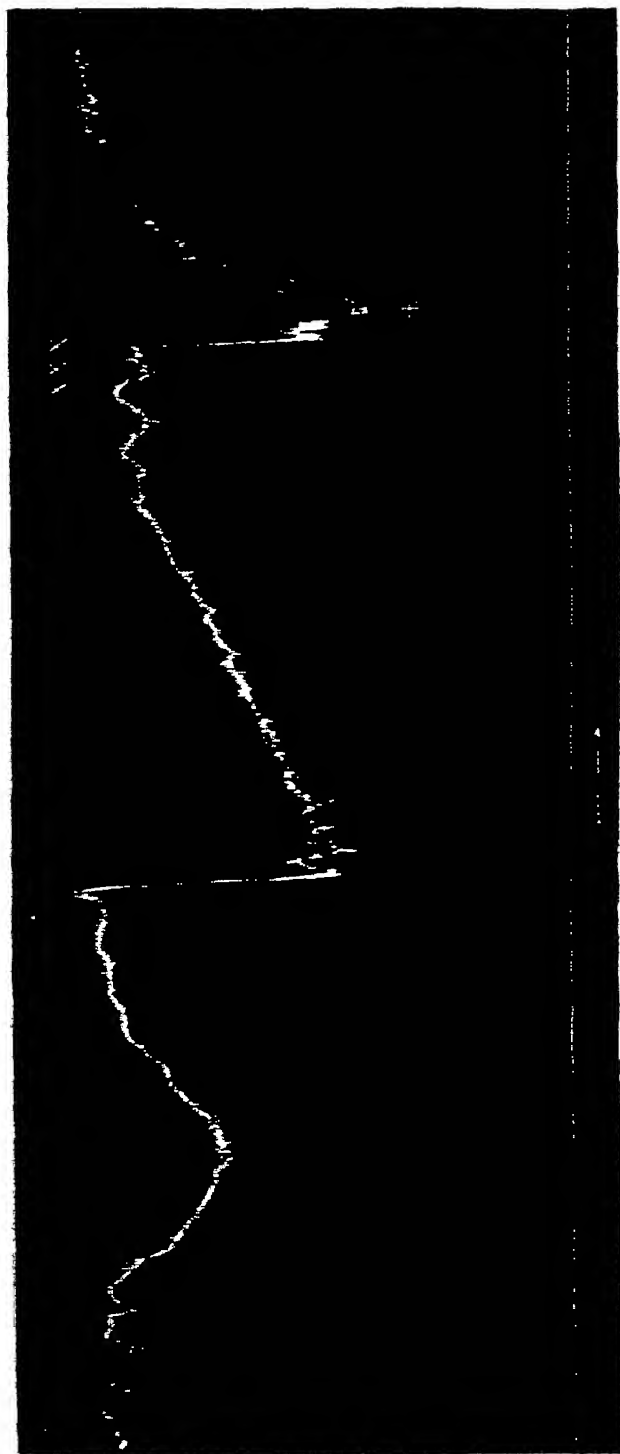


Fig. 31. 85<sup>m</sup> to 120<sup>m</sup>. Showing the result of intravenous injection of 5 minims slowly,\* then of 8 minims of methylbenzene,\*\*\* and, lastly, of 8 minims immediately followed by \*\*\* section of the vagi (see Tracing 30 on quick cylinder).

16 to 10 per minute. The succeeding injection of 10 minims completely paralysed respiration. The heart continued to beat so long as artificial respiration was kept up, and then failed.

*Post-mortem.*—In case quoted, showed great pulmonary œdema.

#### Action of Dimethylbenzene on Circulation and Respiration

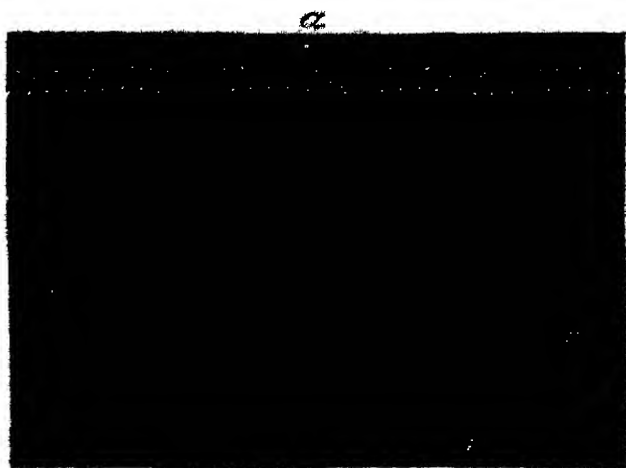


Fig. 32. Quick drum. Time 0. Normal pulse and respiration.

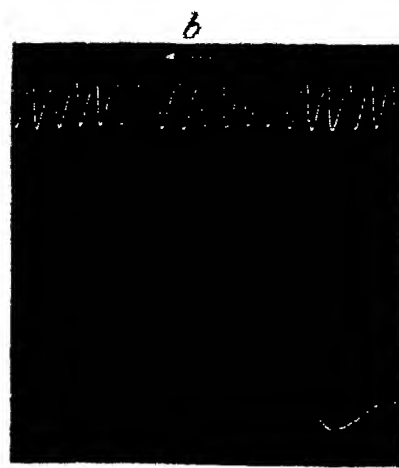


Fig. 33. Pulse and respiration 62<sup>m</sup>

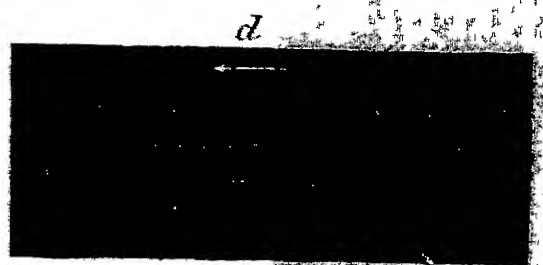


Fig. 34. 98<sup>m</sup>. Vagi not yet divided.

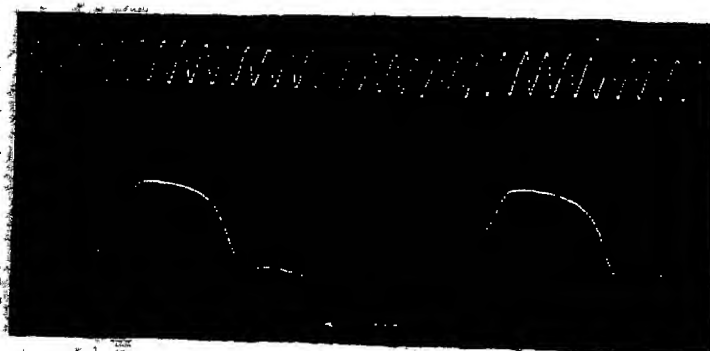


Fig. 35. Time 99<sup>m</sup>. The vagi have been divided. Speed of quick drum 31 millims equal to 5<sup>s</sup>

## Action of Dimethylbenzene on Circulation and Respiration

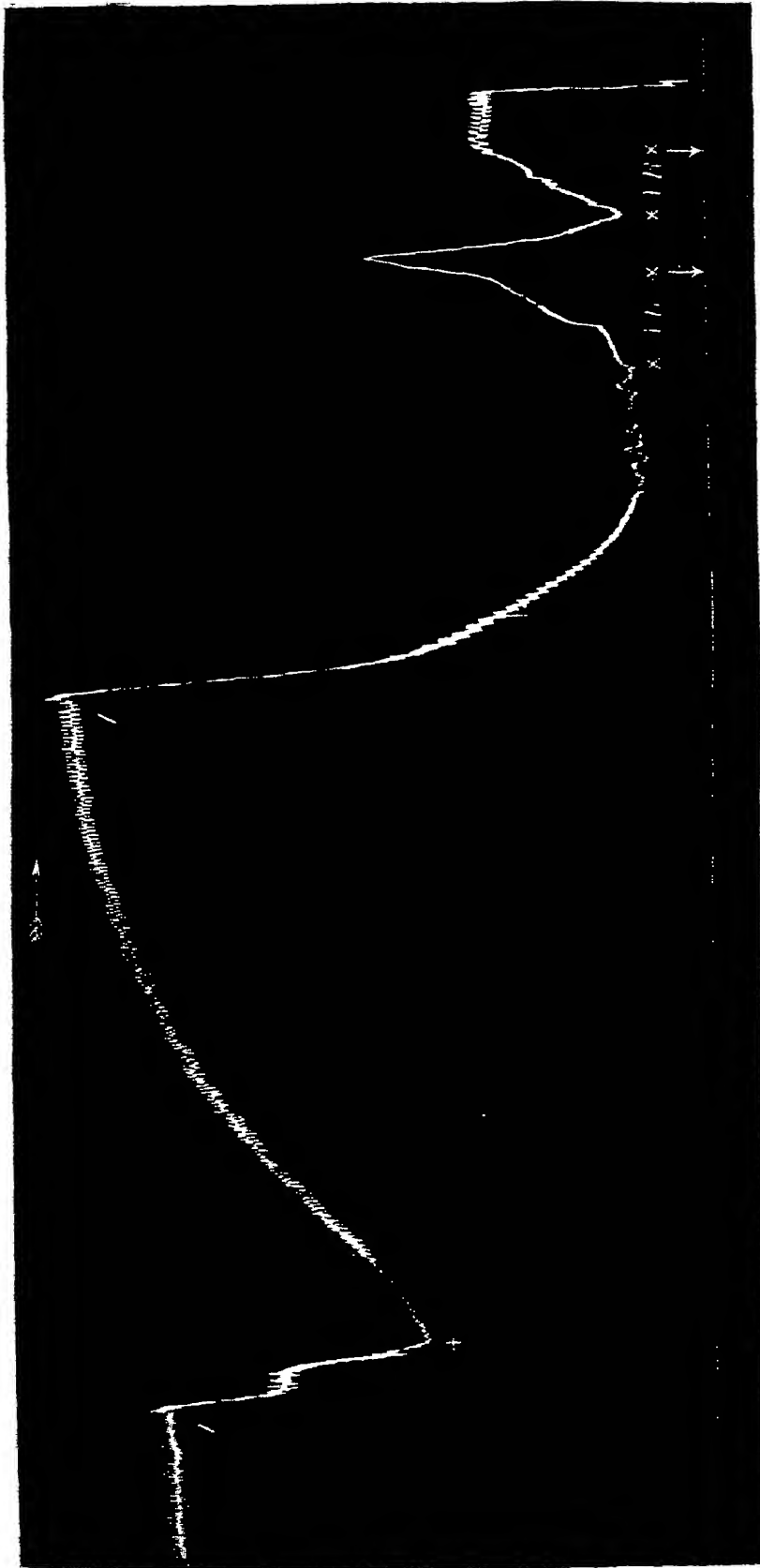


Fig 36. Slow cylinder Blood-pressure tracing of two successive injections of 8 minims dimethylbenzene (I and I'). Vagi divided at + Death occurs on suspension of artificial respiration AR



CAT of 7 lbs Dimethylbenzene Animal in Warm Box to maintain Temperature

Time	Remarks	Pulse for 1 minute	Blood-pressure	Respiration
minutes				
0	(Fig 32)	192	144	25
16	Injected 6 minims dimethylbenzene into intestine	168	140	20
30	Respiratory waves well marked in manometer	.	136	
50				
62	Very distinct wave in descent has developed itself, though it was already discernible at 30 <sup>m</sup> to a lesser extent (33)	168	131	27
65	Ether causes fall of pressure of 33 millims	.	128	
67				
69	Injected 2 minims suspended in 2 c c salt solution into femoral vein			
70	Rise of pressure of 8 millims succeeded by fall to such level			
76	Rise to		130	
77	Injected 4 minims in 2 c c salt solution	..	104	
87	Systole sharp, and shows a second summit in descent of curve	158	120	23
95		.	121	
96	Injected 8 minims suspended in 4 c c salt solution			
98	Blood-pressure falls very rapidly (34) Both vagi divided (35)	140	64	21
100	Prolonged pause in inspiration Pressure rises rapidly	170		10
115			143	
116	Injected 8 minims in 4 c c salt solution At once a fall (36)			
118	All attempts at respiration over	.	13	
123	Artificial respiration raises blood-pressure; when discontinued, death results. Pulse good till artificial respiration discontinued		50	

*Post-mortem*—Some very dark blood in right ventricle A little in the left ventricle No clots here nor in the pulmonary artery. Lungs congested; contain much oedematous bloody fluid

### *Trimethylbenzene (1 2 : 3).*

Injected under the skin trimethylbenzene causes at first a slight fall in blood-pressure, a decrease in the number of cardiac contractions, and an acceleration in the respiration. The pulse then tends to quicken as a set-off to the reduced pressure, and the respiration becomes slower.

Injections of small doses of the drug (largely diluted with salt solution) into the femoral vein cause a slight decline in blood-pressure, an acceleration of both respiration and pulse, but this acceleration is only temporary. The fall of blood-pressure becomes more marked as the amount of the drug in the circulation increases

Section of both vagi, as in experiment quoted, rapidly raises the blood-pressure above its original level, an acceleration of the pulse being well marked The respira-

tion is reduced to half its previous frequency, the long pause in inspiration characteristic of vagotomy being well marked. After further injections the respiration became much embarrassed, a bloody oedematous fluid running freely from the tracheal cannula.

After the last injection spontaneous respiration ceased and artificial respiration failed to raise pressure, death ensuing.

## CAT 8 lbs Trimethylbenzene

Time	Remarks	Pulse for 1 minute	Blood-pressure	Respiration
minutes				
0	(Fig 37)	204	142	36
8	Ether causes fall of blood-pressure			
9	Injected 3 minims trimethylbenzene subcutaneously			
15		180	142	33
30	Injected 30 minims			
35	Distinct second summit after active systole of heart	168	134	48
53	(Fig 38)	192	134	31
72	Injected 2 minims in 2 c.c. salt solution into femoral vein			
80	Injected 6 minims in 6 c.c. salt solution			
82		162	112	42
90	Injected 10 minims in 5 c.c. salt solution		126	
92		108	56	33
	Divided both vagi	168	..	25
100	Indications of second rise in pulse very faint. Long inspiratory pause	180	158	13
122		..	139	
123	Injected 10 minims trimethylbenzene in 5 c.c. salt solution into vein. Fall of 18 millims. blood-pressure. Respiration becomes very laboured. Fluctuations of pressure. Red-tinged oedematous fluid begins to run into tracheal cannula, and secretion of this is soon so rapid that animal threatened with suffocation.			
	(Fig. 39, slow drum, shows course of pressure to end of experiment)			
135		..	111	
140	(Fig 40)	204	110	12
145	Injected 20 minims trimethylbenzene	..	88-100	
148	Artificial respiration fails to raise pressure.			
	Death	.	12	

*Post-mortem.*—Right heart in diastole. Left in systole. Lungs are congested and oedematous. There is a soft clot in pulmonary artery. Kidneys are fatty, congested.

Action of Trimethylbenzene.

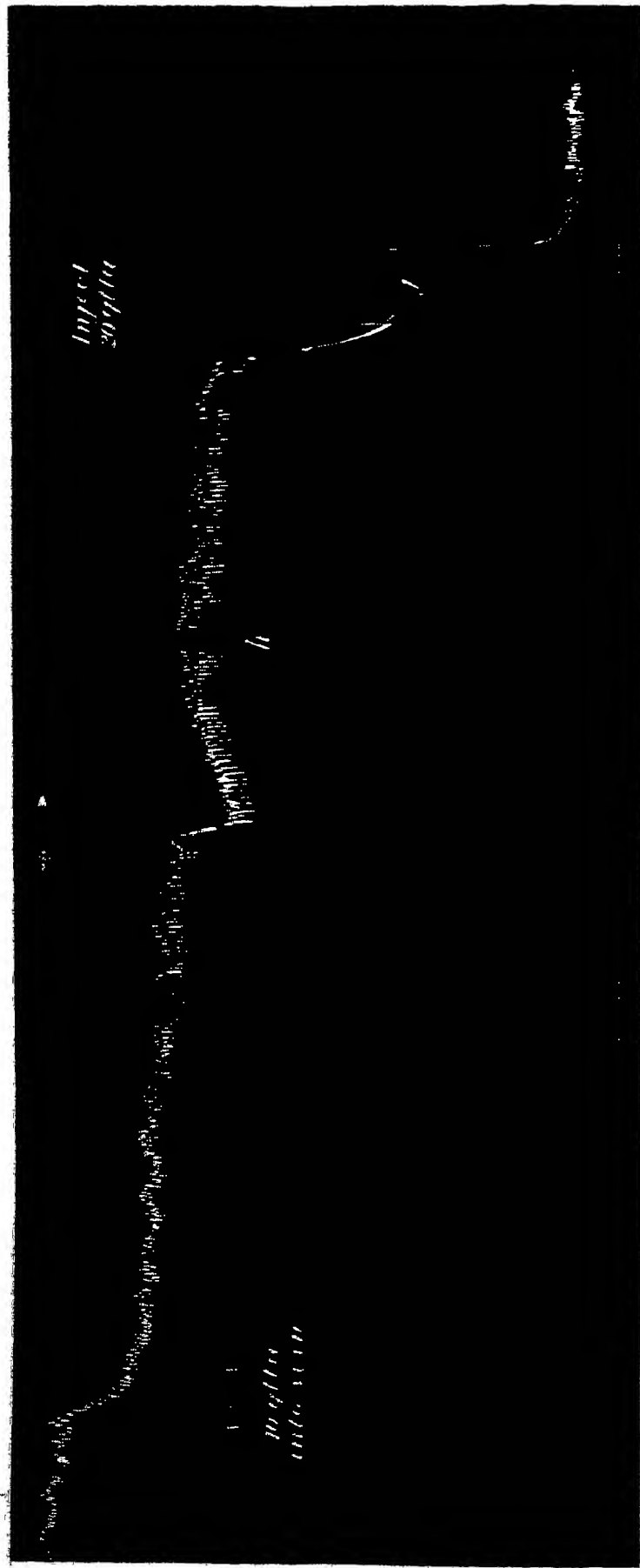


Fig. 39 Last half hour of experiment Vagi divided One injection (intravenous) of 10 minims trimethylbenzene and one of 20 minims rapidly fatal



Fig 37 Time 0<sup>m</sup> Normal pulse and respiration



Fig 38 55<sup>m</sup> After injection of 28 minims of trimethyl-benzene in all

Time of quick drum, 31 mullims. = 5<sup>s</sup>

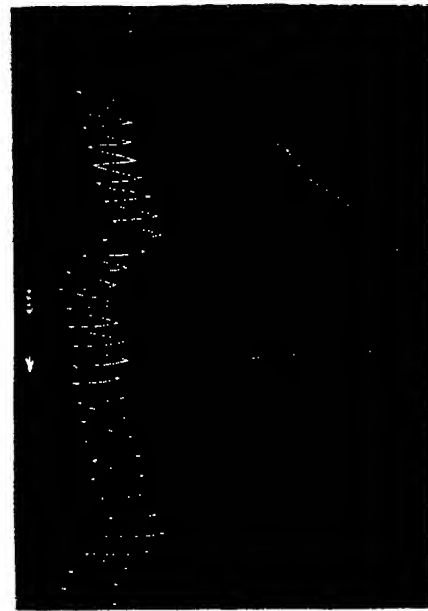


Fig 40 140<sup>m</sup> Vagi have been divided Extreme dyspnoea

*Ethylbenzene.*

When injected into a loop of the intestine, which was subsequently returned to the abdominal cavity, ethylbenzene caused some increase in blood-pressure and also acceleration in the speed of the pulse. A prolonged inhalation of ether reduced this high pressure to or below the normal.

Small doses, 2 to 3 minims, injected into a vein raised the blood-pressure, but larger ones, 5 minims, greatly reduced it, whilst the respiration became much accelerated. The dyspnoea produced by each intravenous injection soon subsided.

*Section of the vagi* only caused a feeble and gradual rise in blood-pressure and produced a very faint acceleration of the pulse. The speed of respiration was reduced to one-half. The respiration and heart both tended to fail, occasional pauses in the former occurring. A few respiratory efforts were made after the heart had stopped.

CAT of 8 lbs., anaesthetised by Ether. Cannulas in Right Carotid, Trachea, and Femoral Vein. Vagi prepared. A Small Loop of Ilium Ligatured and Returned to Abdominal Cavity. Usual arrangement of apparatus.

- 0<sup>m</sup> Original blood-pressure 138 millims. Respirations 14. Pulse 168, there is a considerable pause in inspiration, breathing appeared to be for time altered, owing probably to irritation of vagi (Fig 41.)
- 10<sup>m</sup> Injected 10 minims ethylbenzene into loop of intestine.
- 12<sup>m</sup> Blood-pressure has risen to 140, but rise rapidly reduced by administration of ether
- 17<sup>m</sup> Blood-pressure 120 to 149 (great variation owing to respiratory waves) Respirations 18 (assuming a more normal form) Pulse 192.
- 39<sup>m</sup> Blood-pressure 137  
Injected 10 minims ethylbenzene into ligatured loop of intestine
- 35<sup>m</sup> Fig 42
- 42<sup>m</sup> Blood-pressure rose rapidly to 144 millims Fell slightly and again—
- 50<sup>m</sup> Rose steadily to 143
- 55<sup>m</sup> Ether reduced the pressure rapidly to 117
- 62<sup>m</sup> Blood-pressure 133 Respirations 13 Pulse 162.
- 80<sup>m</sup> Injected into femoral vein 3 minims of ethylbenzene, shaken up with 2 c.c. salt solution
- 85<sup>m</sup> Blood-pressure rose rapidly from 117 to 127, and then fell to 119 gradually; the respiratory waves being very extensive (Fig 46 slow drum.)
- 87<sup>m</sup> Slowly injected 5 minims ethylbenzene, suspended in 4 c.c. salt solution. (c)
- 89<sup>m</sup> Blood-pressure fell rapidly to 62, but soon began to recover itself Respirations 40 Pulse 144
- 91<sup>m</sup> Ligature left vagus. Respirations 29 Pulse 144. (Fig 43.)
- 94<sup>m</sup> Blood-pressure 107.
- 100<sup>m</sup> Blood-pressure steady 109 millims. (c.)  
Injected 5 minims ethylbenzene in 5 c.c. salt solution.
- 102<sup>m</sup> Blood-pressure fell to 46.  
Respirations 28. Pulse 150. The right (remaining) vagus was now tied 5<sup>s</sup> after ligature —  
Respirations 18 Pulse 150.
- 115<sup>m</sup> Blood-pressure only rose very slowly and partially, so that at 115<sup>m</sup> it only reached 81 millims.

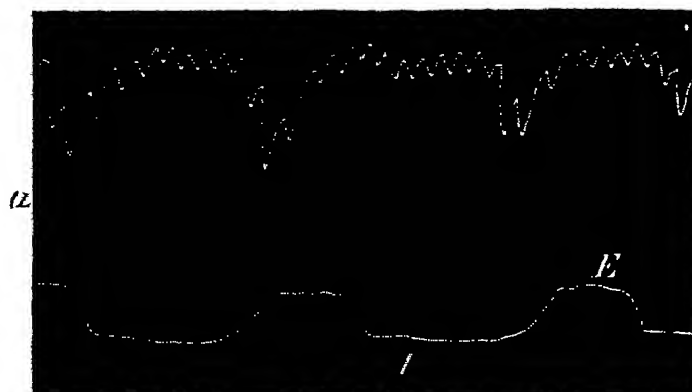


Fig 41. Before injection of ethylbenzene. There is probably irritation of the superior laryngeal nerve provoked by preparation of the vagi

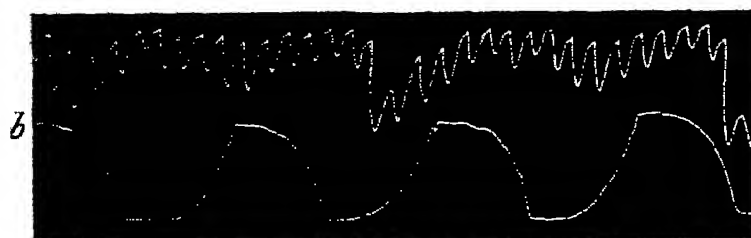


Fig 42 35<sup>m</sup> After injection of 10 minims ethylbenzene into a loop of intestine



Fig. 43. 91<sup>m</sup>. \*Ligature of left vagus. Blood-pressure is low from the preceding injection of 5 minims of ethylbenzene

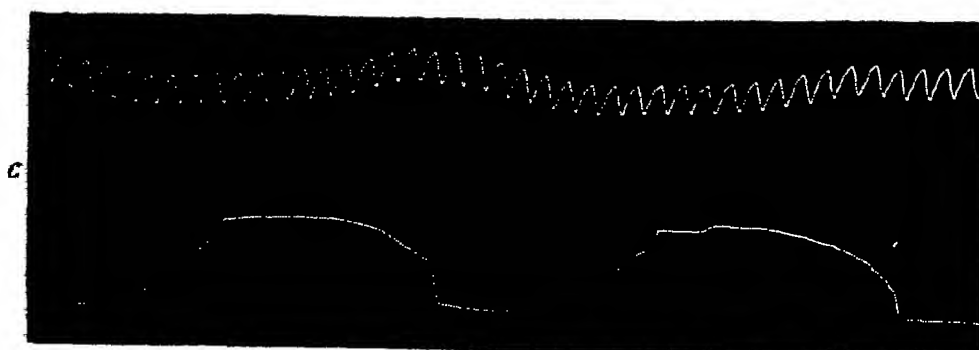


Fig. 44. 115<sup>m</sup>. After ligature of the second vagus

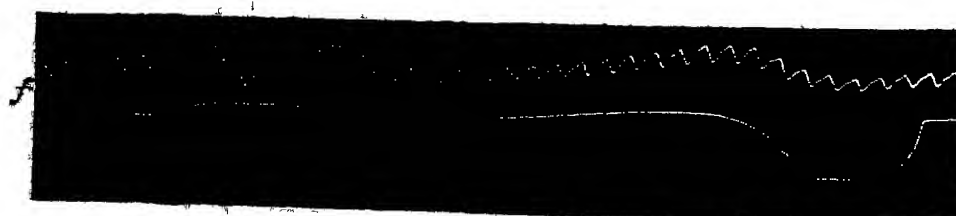


Fig 45. 139<sup>m</sup>. 10<sup>m</sup> before death. Blood-pressure 42 millims

Speed of drum 31 millims = 5°.

## Action of Ethylbenzene on the Circulation

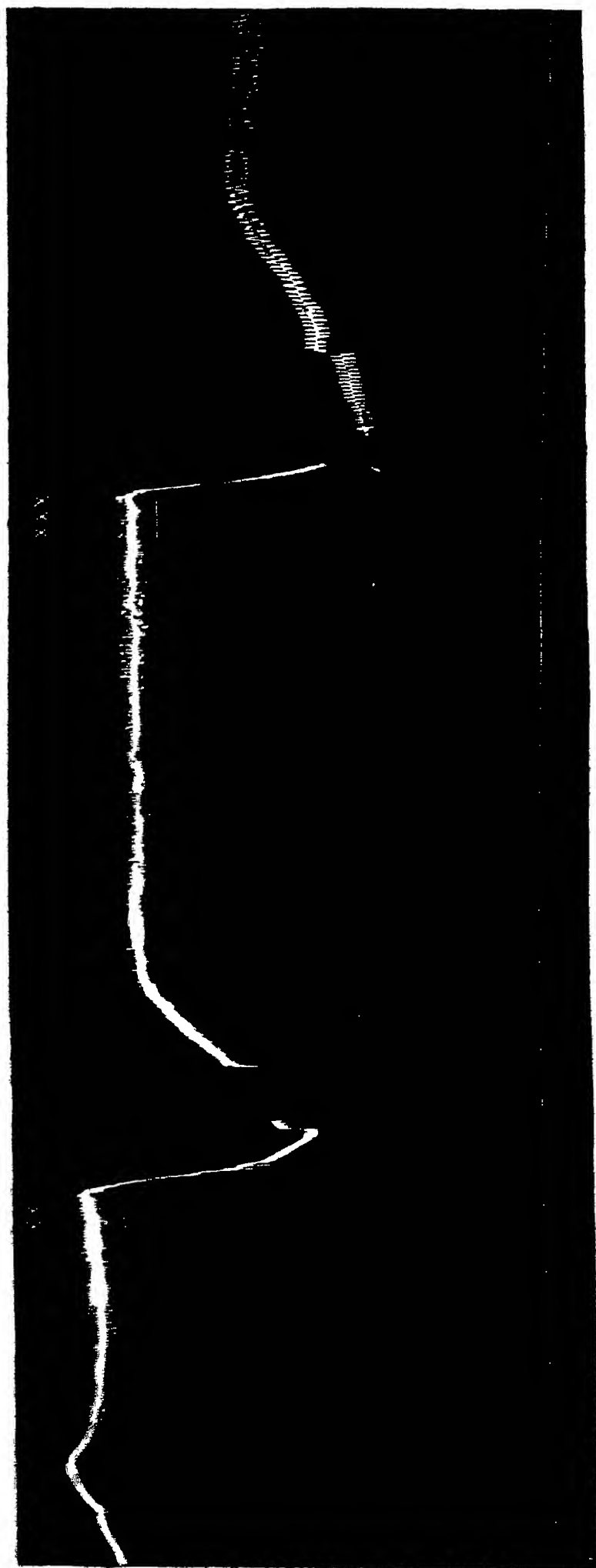


Fig 46. Slow drum. Tracing from 80<sup>m</sup> to 115<sup>m</sup>. Shows three injections of ethylbenzene. The first injection (intravenous) is of 3 minims, the next  $\times \times$  of 5 minims (one, the left vagus ligatured,  $\alpha$ ), the last  $\times \times \times$  of 5 minims (the right vagus ligatured,  $\beta$ )

and thereafter declined. Respirations 7. Pulse 150. The respiratory curves became very well marked and persisted from this time to end of experiment. (Fig 44)

122<sup>m</sup> Blood-pressure 74 millims.

Injected 5 minims ethylbenzene in 5 c.c. salt solution

128<sup>m</sup> The succeeding fall has not been so extensive as formerly, it has now reached 52 millims

130<sup>m</sup> Respiration ceased for 2<sup>m</sup>, its curves in the blood-pressure of course disappearing

132<sup>m</sup> Respiration recommenced

134<sup>m</sup> Respiratory curves reinstated

Blood-pressure 40 millims. Respirations 7. Pulse 150. There is a much longer pause in expiration than before at 115<sup>m</sup>. The fluctuation of blood-pressure holds a somewhat different relationship to the respiration, the maximum corresponding closely with active expiration, whereas before (115<sup>m</sup>) there was a much more distinct rise before the inspiratory pause had terminated.

139<sup>m</sup> (Fig 45)

140<sup>m</sup> Injected 5 minims ethylbenzene quickly. Fall of pressure very slight, respiration slowed

145<sup>m</sup> Blood-pressure 34 millims.

148<sup>m</sup>. 5 minims ethylbenzene injected rapidly caused death in a few minutes.

Respiration outlasted the heart's action.

### *Di-oxybenzene. (Resorcin.) (1 . 3.)*

As in the case of experiments made upon lower animals, we confined our attention to resorcin when studying the action of metadioxybenzene upon Carnivora (Cats)

BRIEGER ('Arch. f. Anat. u. Phys.,' 1879, Sup.-Bd.) has shown that resorcin is not only weaker in its action upon Frogs than its isomers, pyrocatechin and hydrochinon, but that this difference obtains with regard to Rodents. He found that .5 gm. of pyrocatechin was fatal to a Rabbit in 30 minutes, which had survived a dose of 1 gm. of resorcin administered some days previously.

We have carefully examined the action of the drug administered subcutaneously and by injection into the peritoneal cavity.

*Injection into the Peritoneal Cavity.*—For this purpose a 5 per cent solution was made by aid of warm salt solution.

Small doses, .75 c.c., and 2 c.c., had but little effect upon blood-pressure. A slight fall of pressure amounting to from 4 to 10 millims. was produced, but from this recovery took place to a considerable extent, though on repeated injection a permanent reduction remained. In 3 hours' time, after 7.75 c.c. had been injected in all (.38 gm., resorcin), the blood-pressure had fallen from 126 to 110, or through 16 millims. only. The pulse was reduced from 156 to 144, but the respiration was not materially altered; faint twitchings of the thoracic muscles were produced.

Section of the vagi caused a marked rise in pressure, accelerations of the pulse and the usual type of slowed respiration. The effects of such small doses were therefore very slight.

*Subcutaneous Administration.*—Doses of 1 cc. resorcin produced no appreciable effect. After 1.0 gm. had been injected, distinct jerking of the extremities was



noticed in 15 minutes, but this jerking was abolished by deepening the anæsthesia. This first injection, after causing a slight acceleration of respiration, produced a steady fall of 5 per minute, and reduced the pulse by 34 per minute. The blood-pressure fell 14 millims. The jerking which takes place in the muscles of the trunk is itself a factor in producing dyspnœa, as it makes the emptying of the lungs irregular and hinders their expansion. So much is this the case that the rhythm may vary 8 or 10 per minute, according to the depth of anæsthesia. When the animal is deeply narcotised, the respiration becomes slow, though often irregular, with a prolonged pause in inspiration, jerking being abolished. An acceleration in respiration was observed every time that the anæsthetic was relaxed, whilst the returning muscular contractions greatly interfered with the act. The jerking occurred when the animal was entirely unconscious from the action of the ether, and even when the narcotic action which the drug itself causes had been slightly reduced, but under the deeper action of resorcin a condition of narcosis occurred, in which jerking was only very feeble.

There is little doubt, we think, that ether greatly prolongs life in poisoning with resorcin, by reason of the power it possesses of relieving and steadying respiration. In the experiment we are about to quote, we administered to a Cat of 6 lbs. no less than 3 grms of resorcin in the course of 3 hours, and at the expiration of 5 hours, when the experiment terminated, the blood-pressure was still 74 millims.

DIOXYBENZENE on Blood-pressure of Cat. Cannula in Trachea. Cannula in Right Carotid Artery. MAREY'S Tambour on Chest. Ordinary Connection with Mercurial and FICK'S Manometers.

0<sup>h</sup> 0<sup>m</sup>. Experiment commenced

30<sup>m</sup>. Blood-pressure varies from 120 to 128 millims, and is rather easily reduced by ether. The pulse averages 184 and the respiration 42 per minute (Fig. 47)

35<sup>m</sup>. *Injected 1 grm. of resorcin dissolved in 20 c c salt solution subcutaneously*

48<sup>m</sup>. Jerking of muscles of limbs and trunk has commenced. Blood-pressure 116 millims. Pulse 180. Respiration, 54.

A small clot formed in the cannula immediately after taking the tracing

60<sup>m</sup>. Blood-pressure 113. Pulse 172 (fig. 48). Respiration about 60, but, owing to jerking, estimation is difficult. Urine passed, but has no abnormal odour. Jerking easily subdued by ether, and respiration reduced to 40. (Fig. 49)

67<sup>m</sup>. Blood-pressure 110. Pulse 156. Respiration 36.

82<sup>m</sup>. Pulse 156; appears to be unaltered by ether, whilst jerking abolished and respiration slowed by it

110<sup>m</sup>. Blood-pressure 102. Pulse 150. Respiration 37.

113<sup>m</sup>. *Injected 1 grm. of resorcin in two places as above.*

128<sup>m</sup>. Jerking very powerful, but disappears when deeply anæsthetised. Blood-pressure 96.

150<sup>m</sup>. Blood-pressure (94) is very steady, except for gradual tendency to fall.

160<sup>m</sup>. Pulse 146 per minute.

175<sup>m</sup>. *Injected 1 grm. of resorcin in two places as above.*

- 183<sup>m</sup> Blood-pressure 95 millims. Pulse 140 Respiration 40, irregular
- 197<sup>m</sup> Blood-pressure 90 Pulse 108 (fig 50) Respiration 30, pause in inspiration  
At this time the temperature in the rectum was reduced to 29° 5 C, though the laboratory was warm and the animal had been kept carefully covered by cloths
- 210<sup>m</sup>. Though ether has been suspended for 20 minutes, the animal is completely narcotised; muscular jerking has greatly diminished No clotting has occurred for nearly three hours The respiration is superficial Pulse 108 Pressure 84 millims  
Powerful sensory stimulation of sciatic nerve causes a rise of blood-pressure of 4 millims, but on second application had no effect
- 245<sup>m</sup> Blood-pressure 76 Pulse 108 The respiration is feeble, and is still marked by the twitchings of thoracic muscles
- 270<sup>m</sup> Pressure 74 Pulse 96 Respiration very irregular (Fig 51)
- 275<sup>m</sup> Both vagi divided
- 278<sup>m</sup>. Pressure 66 Pulse 90 Respiration 14, extremely feeble and failing
- 285<sup>m</sup> The experiment was now terminated

*Trioxylbenzene (1 : 2 · 3, Pyrogallol)*

As this is a soluble salt, no mechanical difficulty was found in its administration. A 10 per cent. freshly-prepared solution was employed, and the desired dose of this was largely diluted with salt solution, for the purpose of subcutaneous or intravenous injection.

Subcutaneous injections of .065 grm. were not succeeded by any great change in pulse or blood-pressure beyond a slight slowing of the former and fall of the latter. The respiration, however, was distinctly slowed

Intravenous injections of amounts varying from .033 to .065 slowly made into the femoral vein, were rapidly succeeded by a marked rise of 6 to 13 millims of pressure; this rise, after persisting for 2 to 5 minutes, was followed by a fall to the previous level. The cumulative action of the drug was shown by a gradual, but steady, fall of pressure after a total dose of .12 grm. had been injected.

Larger doses of .4 and .6 grm., well diluted and slowly injected, caused also a rapid rise of pressure; but this rise quickly reached its maximum, and the pressure fell much below the previous level. During this fall respiration was very slow, a long pause in expiration being succeeded by a rapid and incomplete inspiratory movement. The heart beat only at the rate of 19 per minute for some time after the large injection; the systole was sharp, and succeeded by what appeared to be a second feeble contraction passing into a prolonged diastole. As the immediate effect of the drug passed off, this second cardiac effort developed still further, so as to give a bigeminal character to the pulse, and gradually the previous rhythm was restored. After 1.252 grm. in all had been injected, in the experiment quoted, the blood-pressure gradually fell, the respiration declined and ceased simultaneously with cardiac action.

Action of Dioxybenzene 1 3 Resorcin

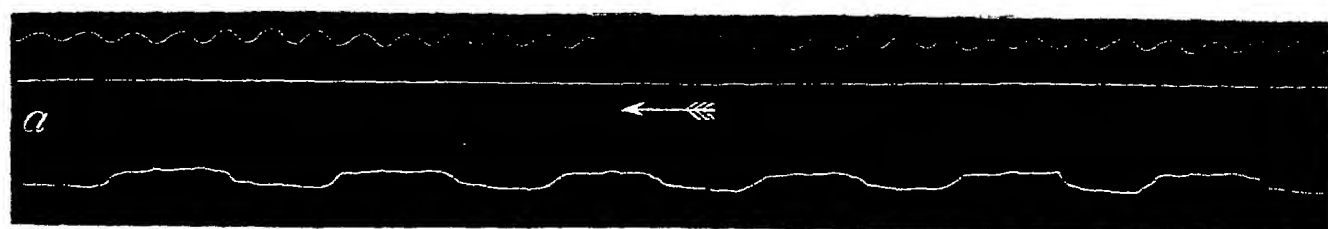


Fig 47 Before injection of Resorcin



Fig 48 Time 60<sup>m</sup> 1 grm of Resorcin injected 25<sup>m</sup> previously



Fig 49 Time 62<sup>m</sup> Deep anæsthesia

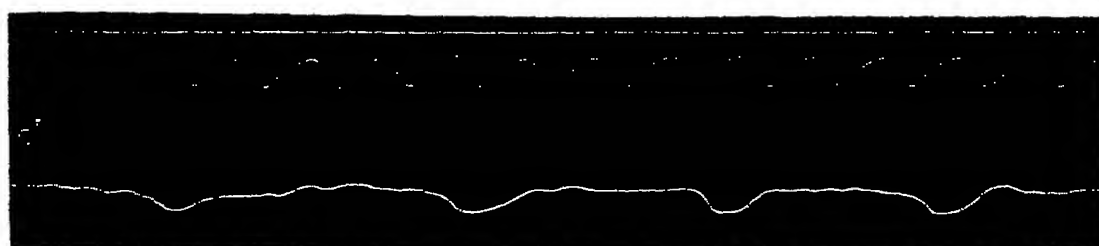


Fig 50. Time 195<sup>m</sup> Three grms. of Resorcin have been injected



Fig. 51. Time 270<sup>m</sup>.

Speed of drum, 64 millims. = 5<sup>s</sup>.

CAT of 7 lbs Ether was used as an Anæsthetic Animal placed in Warm Box  
 Cannulas were placed in the Right Carotid, Femoral Vein, and Trachea  
 Immediately after placing the animal in position the Heart suddenly failed,  
 though but little Ether had been given, and Pressure fell from 134 to 22  
 Artificial Respiration restored Animal.

Time	Remarks	Pulse for 1 minute	Blood- pressure	Respiration
minutes				
0	(Fig. 52)	180	124-130	32
17	Injected 10 minims of a 10 per cent solution of trioxybenzene			
35			121	
50			102	
62	Much tremor of hind legs	158	94	24
73	Blood-pressure risen under ether Respiratory blood-pressure waves become very large	181	102	15
76	Injected 2 minims diluted with 2 c.c. salt solu- tion. Rise of 5 millims. in the pressure			
80	Injected 5 minims, 10 per cent. solution			
82	Blood-pressure risen 6 millims., falls rapidly to former level			
90	Clot far down in right carotid artery. Insert cannula into left carotid. (15 <sup>m</sup> lost)			
105	Injected 10 minims of a 10 per cent. solution as before (fig. 53)	156	93-106	24
110	Both vagi divided. No rise of blood-pressure (fig. 52)	156	..	23
112		..	84	
115	Injected 10 minims of a 10 per cent. solution as before (fig. 54)		96	
118		150	64	19
122		157	76	17
124	Injected 1 grm. in 3 c.c. salt solution Rise of 16 millims. succeeded by fall	156	..	19
130	Injected 4 grm. in large solution (fig. 54, <i>d</i> <sup>x</sup> )	165	76-82	23
135	Pressure begins to rise again	..	51	
142	Injected 6 grm. trioxybenzene (fig. 54, <i>d</i> <sup>x</sup> )	19-73	79-22	3-6
146		168	36	11
150	(Fig. 55)	..		
158		..	23	
179	Heart stopped For some time before death there was no indication for ether			

*Post-mortem.*—Lungs pale Heart in diastole; on cutting much dark blood escaped and ventricle  
 commenced active ventricular movement. Intestines pale, peristalsis active Kidneys congested.

Action of Trihydroxybenzene 1 · 3 Pyrogallol Experiment on a Cat

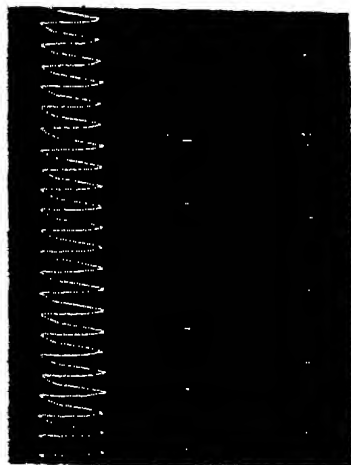


Fig. 52. Quick drum. Normal pulse and respiration.

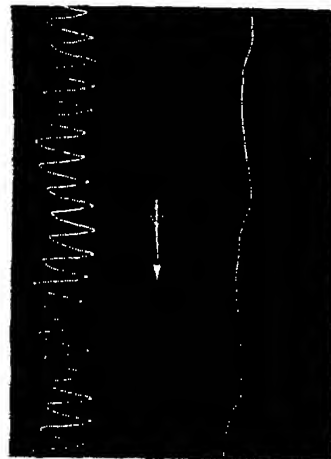


Fig. 53 Quick drum. After injection of pyrogallol

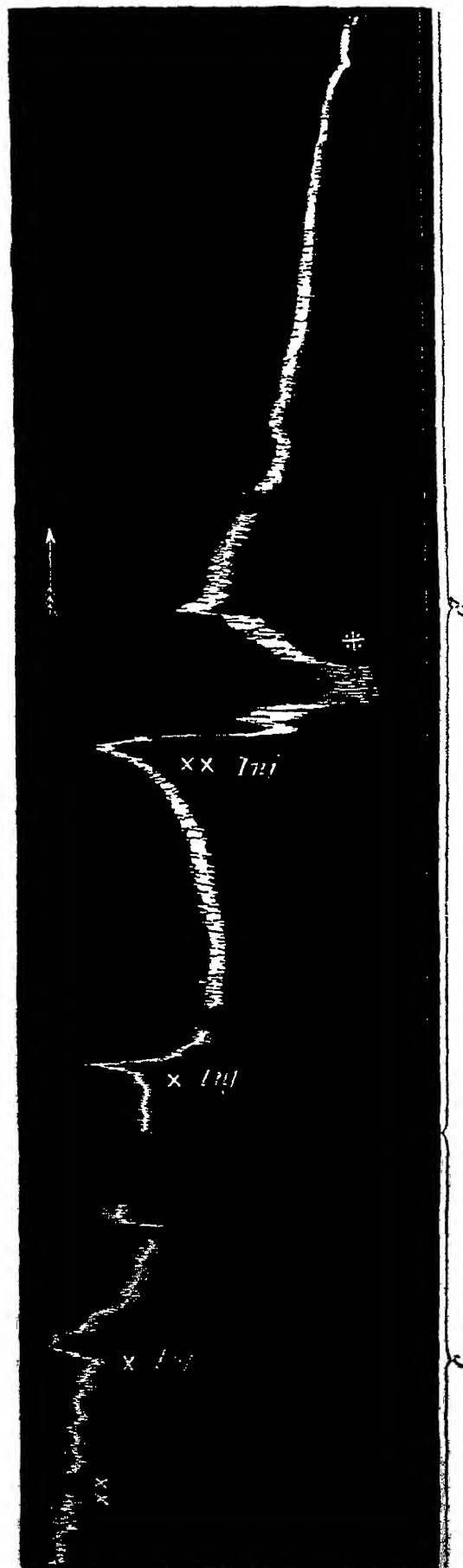


Fig. 54 (c) Slow drum Injection of .05 gram of pyrogallol (both vagi cut)  
(d) Slow drum Shows the effect of injection of .4 gram and of 6 gram pyrogallol  
For \* see fig 55



Fig 55 Quick drum Tracing taken at \*, showing great slowing and irregularity of the heart succeeded by recovery

*Amidobenzene (Anilin)*

Many experiments were made with this drug, the mode of administration being varied.

Intravenous injection produced a slight rise of pressure, when  $\frac{1}{2}$  minim of anilin largely diluted was employed; when the dose was increased to 2 minims a much more distinct rise was observed.

Large doses of 1 c c caused a marked fall of blood-pressure. When introduced subcutaneously, or into the stomach, no rise of blood-pressure was observable, though the fall was slow in developing. In one case of subcutaneous administration of 1.25 c.c. in one dose to a Cat of  $5\frac{1}{2}$  lbs although death resulted in 2 hours 10 minutes, the fall of pressure during the first 40 minutes was quite insignificant.

After absorption has taken place to some extent marked tremors develop, and even jerking of the trunk and limbs, which disappear when the narcosis is rendered very deep. The vagi remain active till the last.

Respiration is greatly slowed and a long pause occurs in inspiration. Section of vagi at this stage has an additional effect in slowing the breathing.

The heart is at first somewhat slowed, but is quickened before death. A systole is succeeded by a diastole which is often cut short midway by a second systole, such a rhythm, consisting of a bigeminal systole alternating with a single beat, was in one instance persisted in for a considerable time.

The production of TRAUBE'S curves was observed several times as a result of the administration of anilin; these curves were reduced in extent, but became more frequent on exposing the intestines to the air.

After death the irritability of the muscular tissue was found to be greatly impaired.

## CAT of 6 lbs Subcutaneous injection.

Time	Remarks	Pulse for 1 minute	Blood- pressure	Respiration
minutes				
0	(Fig 56)	216	145	25
20	Injected 10 drops amidobenzene			
28	.	216	145	18
45	Injected 10 drops amidobenzene			
56	Character of pulse changed, a distinct second wave in descent appearing (fig 57)	204	137	22
82	Ether causes fall of 38 millims			
85	Same character of pulse as at 56 <sup>m</sup> , though showing higher tension No more amido-benzene has been injected	214	130	30
90	(Fig 58)			
100	Steady fall of blood-pressure (fig 59)			
112	Inject 20 drops as before			
116	.	212	100	28
145	Periodic rise of blood-pressure, corresponding with powerful inspiratory movement with long pause in inspiration Pulse shows peculiar variation in second notch of descent (fig. 60) Slow drum		60	
155	Both vagi now divided. Temporary rise of pressure. Curves persist (fig 60)			
170	Rise of pressure consonant with deep inspiration already mentioned Sinking of pressure occurs as soon as inspiration relaxes The other inspiratory jerk appears to be abortive.	200	..	13
180	After long inspiration has relaxed, there are few rapid inspiratory movements, and these become more seldom till the next deep inspiration	..	40	
190	Curves persist. Pressure declining very slowly			
200	Stimulating sciatic raises blood-pressure very slightly, 4 millims (fig 61) Stimulating vagi lowers blood-pressure slightly (9 millims)	..	34	
215	Opened abdominal cavity and exposed intestines thoroughly, mesenteric vessels are found to be contracted (fig. 62) Exposure destroys the marked waves which have so far existed, though respiratory waves appear, the pressure does not rise as before	196	30	
227	.	174	22	
250	A further attempt at respiration still observed		0	

*Post-mortem.*—Intestines very empty of blood, no peristalsis Hardly any local contraction or stimulation. Both sides of heart dilated with dark blood. Lungs very pale and putty-like in appearance. Muscle gave only very feeble tetanus to direct and indirect stimulation





Fig. 56. Pulse before injection.



Fig. 57. 5 5m. After total subcutaneous injection of 20 minims



Fig. 58. 90m. Total injection still 20 minims.



Fig. 59. 100m. After total subcutaneous injection of 40 minims

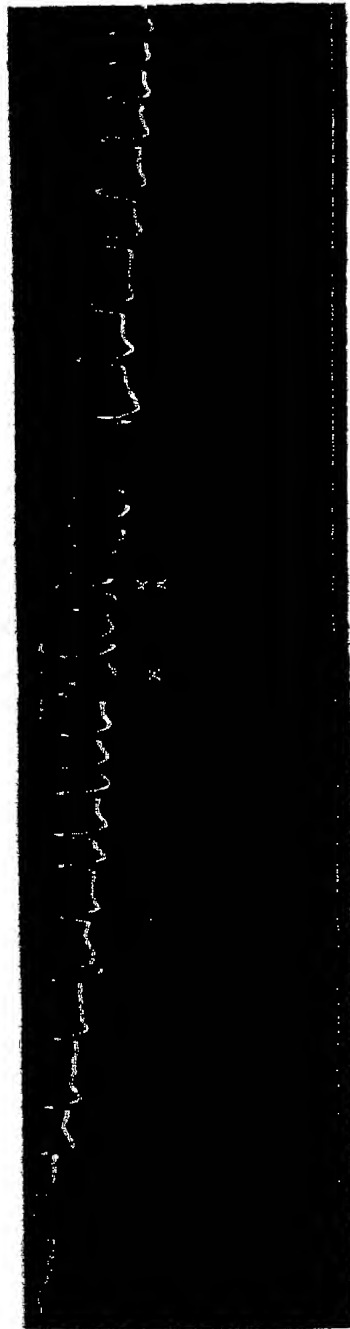


Fig. 60. 145m to 170m. Showing vaso-motor fluctuations of blood-pressure before and after section of the vagi.

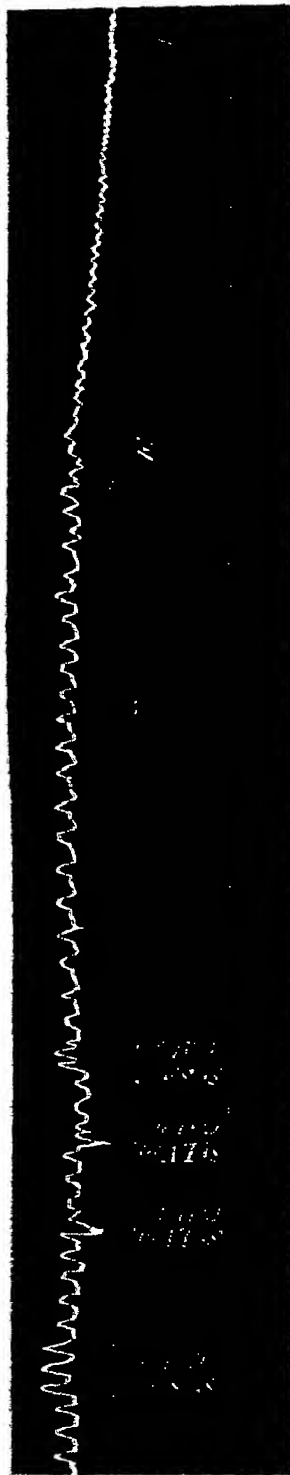


Fig. 61. 195m to 225m. Stimulation of sciatic and vagi. Exposure of intestines with resulting change in wave.

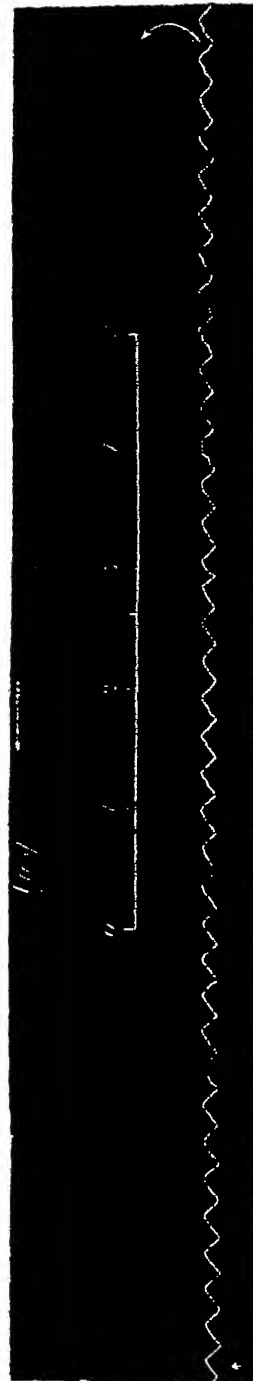


Fig. 62. 218m. Shows respiration and its effect on blood-pressure

*Nitrobenzene.*

Small doses (one to two minims of nitrobenzene) cause a slight fluctuation in blood-pressure usually in the direction of a fall ; larger doses, 4 to 10 minims, cause a marked fall of blood-pressure. This fall, from which the recovery is only very gradual, is associated with great slowing of the pulse. When the vagi are divided during such a condition, a marked rise in the frequency of the pulse with elevation of the blood-pressure takes place, but a repetition of the injection may even then cause a distinct fall of pressure and slowing of heart

The respiration was not found to be markedly affected in rate, the experiment quoted shows limit of variation of 8 per minute up to the time of division of the vagi ; a marked acceleration occurred before death, however, even after vagotomy, and the respiration distinctly outlasted cardiac systole

The form of the pulse was modified throughout by the action of nitrobenzene, the systole became slower and more gradual with a sustained maximum, whilst the diastolic relaxation was distinctly prolonged ; this pulse can be scarcely considered indicative of a peripheral relaxation of the vessels, though, presumed a certain amount of pulmonary obstruction, which the post-mortem appearances seem to justify, the venous congestion may have served to mask the change in the arterioles.

Administration of 62 drops in the course of 3 hours of nitrobenzene was fatal to the animal in question.

This benzene compound is certainly one of the most active we have examined with reference to its action upon the heart.

## CAT of 7 lbs. Usual arrangement of apparatus

Time. minutes	Remarks	Pulse for 1 minute	Blood- pressure	Respiration
0	Blood-pressure lowered from commencement by inhalation of ether (fig 63) . . . . .	152	110-120	40
10	Inject 1 minim nitrobenzene into femoral vein in 2 c c salt solution			
11	. . . . .	..	Slight rise followed by little fall	
30	Injected 2 drops		Fall of 3 millims	
54	Injected 4 minims in 3 <sup>m</sup> (in 5 c c salt solution) An occasional very extensive excursion above or below the abscissa is seen . . . . .	..	Gradual fall of 6 millims.	
67	Injected 10 minims in 5 <sup>m</sup> as before Total fall resulting amounts to 42 mm., a tendency to recovery occurs before completion of injection Excursions very extensive Systole long maintained (Fig 64, slow drum) . . . . .	96	104-62	36
70	(Fig. 65)	..	97	
80	. . . . .	132	80	44
100	Decided tendency of pressure to fall Systole long maintained . . . . .			
108	Rapid injection of 10 minims Long respiratory pause in inspiration Maximum of pulse pressure long continued, one or more waves in descent . . . . .	107	Fall of 28	36
112	(Fig. 66)			
113	Divided both vagi, rapid rise of blood-pressure commenced . . . . .	132	52	26
118	. . . . .	144		
122	(Fig. 67). Slow drum and quick drum (fig 68)	..	103	
123	Inject 15 minims (in large drops not well shaken up)			
126	Excursions of mercury extensive. Recovery very gradual . . . . .	..	65	
135	Strong stimulation of vagus . . . . .	..	Fall of 31	
138	Injection of 20 minims nitrobenzene not in emulsion			
143	Death . . . . .	..	Rapid fall of 52 millims	44-60 very irregular
	Just before death (fig. 69) . . . . .	104	17	44-60 very irregular
	Respiration outlasted pulse.			

Post-mortem.—Right heart dilated, full of dark blood, smelling strongly of nitrobenzene Left heart in systole. Lungs contain much frothy fluid; seem cedematous. No paralysis of nerves or muscles. Peritoneum of intestine. Vessels of mesentery dilated.

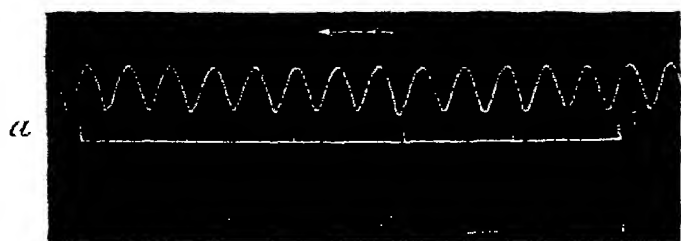


Fig 63 Quick drum Pulse and respiration before injection of nitrobenzene

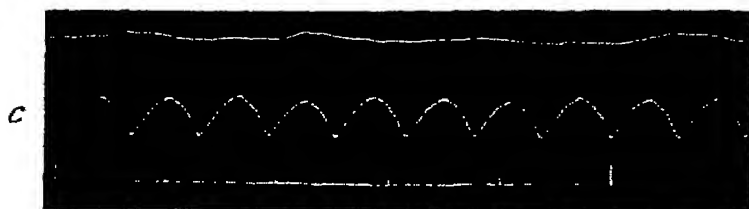


Fig 65. At 70<sup>m</sup>, immediately after the intravenous injection of 10 minims of nitrobenzene (17 minims in all previously injected)



Fig 66 At 112<sup>m</sup> (27 minims in all previously injected)

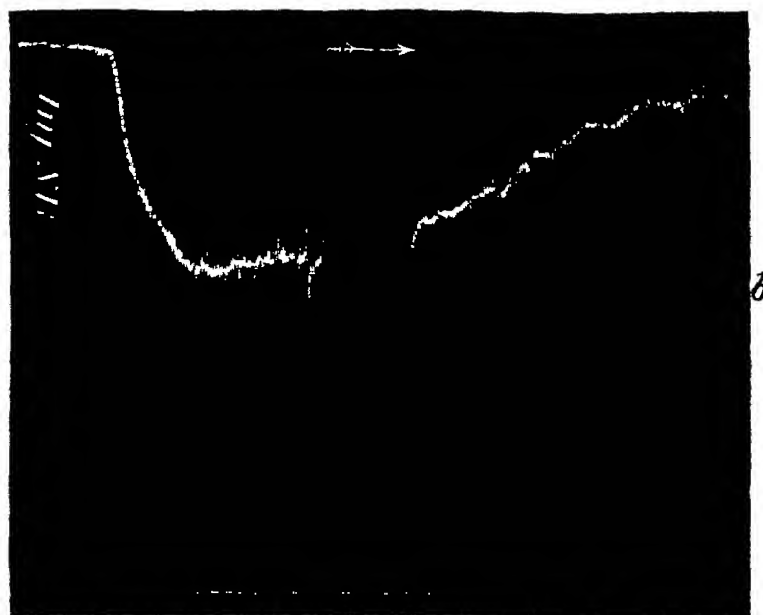


Fig 64 Slow drum. Blood-pressure 65<sup>m</sup> to 80<sup>m</sup> Injection of 10 minims nitrobenzene

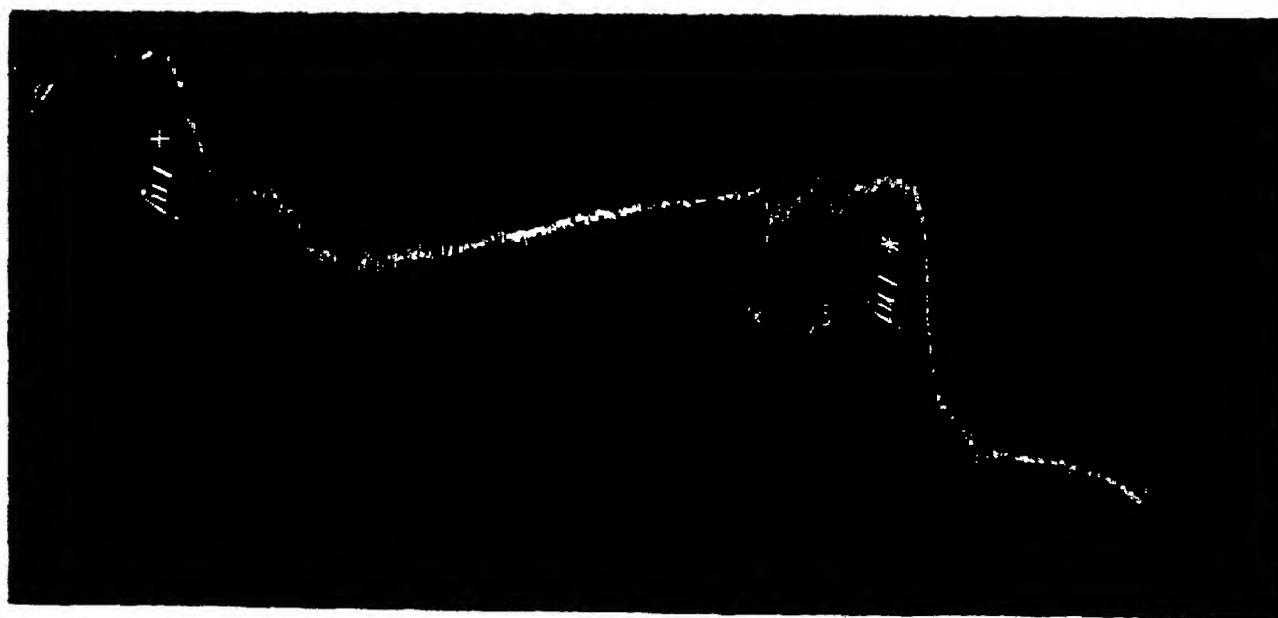


Fig 67 Slow drum Blood-pressure 122<sup>m</sup> to 140<sup>m</sup> Vagi already cut. Final injections of nitrobenzene 10 gtts. (+) and 20 gtts. (\*). *a.* Stimulation of vagus, coil 4 centims *β* Stimulation, coil 0.



Fig. 68. At 122<sup>m</sup>. After section of both vagi.



Fig. 69. At 143<sup>m</sup>. Just before cessation of heart.

Speed of quick drum 55 millims. = 5<sup>s</sup>.

" slow " 19.4 millims. = 5<sup>m</sup>.

## COMPARATIVE ACTION OF BENZENE AND ITS COMPOUNDS ON RESPIRATION, BLOOD-PRESSURE, AND PULSE

### *Respiration.*

#### *Benzene and the Halogen Compounds.*

An alteration of respiration was an early effect of the drugs. This acceleration has been observed to vary in degree with the different bodies.

*Intravenous* injection of aromatic benzene caused a slight acceleration, but ultimately a great slowing of respiration, whilst subcutaneous injection caused from the first a steady decline. Monochlorobenzene produced a very decided acceleration of respiration by whichever way administered, followed by slowing, and in all the experiments made, respiratory arrest was not the immediate cause of death. Monobromobenzene caused also marked respiratory acceleration in the first instance and then depression, but the respiratory movements outlasted cardiac systole.

Monoiodobenzene was not so active in causing acceleration, nor was the retardation of respiration by any means so marked as with the other halogen compounds.

In all cases the greatest acceleration occurs after intravenous administration.

#### *The Compound Benzenes possessing Alcoholic Radicles*

*Methylbenzene*, whether by intravenous or hypodermic administration, accelerates the respiration in the first instance and then slows it. Pulmonary oedema was induced probably from capillary embolism caused by the compound in the lungs.

*Dimethylbenzene* acts powerfully also on respiration. A short period of slowing followed intestinal absorption of the drug, then an acceleration, and ultimately, however administered, the respiration became greatly slowed. Pulmonary oedema tended to occur after intravenous injection, but artificial respiration was capable of prolonging life, the heart beating moderately well after all natural attempts at respiration ceased.

*Trimethylbenzene*, by intravenous and hypodermic injection, produced an acceleration of respiration, then a slowing which was still further increased after vagotomy. Death occurred here also from pulmonary oedema and arrest of respiration.

*Ethylbenzene* likewise accelerated respiration, and this to a considerable extent when intravenous injection was made, though recovery towards the normal tended to occur soon afterwards. The heart, however, failed before respiration.

#### *Hydroxy Compounds*

*Dicarbonylbenzene (Resorcin).*—Hypodermic administration slightly slowed the respiration; dyspnoea was produced, apparently as a result chiefly of jerking of the thoracic muscles which the drug induces, as it is to a great extent removed by deepening the

anæsthesia A marked slowing of the respiration was ultimately caused by resorcin. The respiration tended to cease somewhat before the heart.

*Pyrogallol* 1 2 3 —Appeared from the first to slow respiration, this retardation being specially marked after intravenous injection. A tendency to an expiratory pause was observed.

*Respiration* ceased simultaneously with the heart.

*Amidobenzene* caused some acceleration of respiration with changes in its character, succeeded by a decided slowing. The respiration was greatly reduced by double vagotomy.

Feeble respiration occurred during fall of pressure, and thoracic movement slightly outlasted cardiac contraction.

*Nitrobenzene* did not greatly affect respiratory rhythm, though ultimately some slowing with long pauses in inspiration supervened. Double vagotomy caused a marked slowing, but on further injection the respiration again became rapid and outlasted the pulse. Some œdema of the lung was found after death.

### *Pulse and Blood-pressure.*

*Aromatic benzene* produced in the first instance but a slight effect in the direction of raising the blood-pressure and slowing the pulse, with a tendency to irregularity and incomplete systole. Section of the vagi was followed by a rise of blood-pressure with cardiac acceleration. Death was due to cardiac arrest.

### *The Halogen Compounds*

*Monochlorobenzene* showed considerable activity in the earlier part of its action, in raising the blood-pressure and accelerating the pulse. Cardiac arrest was the cause of death.

*Monobromobenzene* in small doses subcutaneously, and in small doses slowly injected into veins, caused an elevation of the blood-pressure with some acceleration of the pulse. Both these effects were weaker than after monochlorobenzene. Rapid injection of even a small quantity occasioned a marked fall in the pressure. Death was due to cardiac arrest.

*Moniodobenzene* caused marked cardiac acceleration of the pulse after intestinal administration, the pressure also rising. An increase of pressure and pulse rate was produced by vagal section. Death was due to cardiac failure.

*Methylbenzene*.—A marked acceleration of the pulse with a rise of pressure resulted from the earlier action of this drug. Large doses reduced both and rendered the pulse irregular. The pulse was accelerated by vagotomy. Cause of death, pulmonary œdema.

*Dimethylbenzene*.—Whilst intestinal injection of this drug reduced the pressure to a slight degree, intravenous injection of the emulsified body in very small doses

produced a very slight rise of pressure, whilst doses of 4 minims and upwards, even freely diluted, caused a marked fall. Larger injections reduced blood-pressure, but the heart outlasted respiration.

*Trimethylbenzene*.—Small doses, both by hypodermic administration and intravenous injection, slightly reduced the pressure, whilst an acceleration of the pulse was observable. The pulse by the former method was slowed, by the latter somewhat accelerated. Section of vagi raised pressure and accelerated the pulse, after the period of depression had been produced. This appears to be the most active of the methyl compounds.

*Ethylbenzene*.—In small doses, both by intestinal and intravenous administration, this drug caused an elevation of blood-pressure and acceleration of the pulse. Large doses produced a rapid fall of pressure with slow recovery. This effect was to some degree central, as division of the vagi caused some rise and acceleration.

*Dioxybenzol (Resorcin)*.—Caused some fall of pressure and slowing of pulse, but neither effect well marked except with very large doses. A great slowing of the pulse ultimately ensued.

*Pyrogallol*.—Small doses to some extent reduced pulse and blood-pressure. Injections were succeeded by a rise, which suddenly gave place to a considerable fall from which recovery was comparatively slow. The pulse became very slow, of irregular rhythm and peculiar form.

*Amidobenzene (Anilin)*.—From the subcutaneous cellular tissue and the stomach this compound produced a slowly developing fall of pressure, the heart being slowed. Intravenous injection, however, caused a rise of pressure if the dose was only a small one, 1–2 minims. After a single large dose, or repeated small doses, a great fall in pressure took place.

*Nitrobenzene*.—Small doses caused a fluctuation in the blood-pressure usually in the direction of a fall. Large doses greatly reduced the pressure and slowed the pulse. Section of the vagi during the effect caused a rise and acceleration, but further injection caused a fall and slowing. Death was from cardiac failure.



IX *Contributions to the Chemical Bacteriology of Sewage*

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[PLATES 40-43]

THE present paper contains the results of the chemical and bacteriological examination of sewage, with the object, in the first place, of ascertaining the species of organisms therein contained, and, in the second, of determining some of their chemical characteristics.

Of late years attention has chiefly been paid to the study of pathogenic organisms, whilst the far more numerous class of saprophytic organisms, which, although not associated with disease, nevertheless play a most important part in nature, has only been examined by a few investigators.

The great progress which has recently been made in our knowledge of pathogenic processes from a bacteriological point of view is, to a great extent, due to the method of plate culture on solid media, proposed by KOCH, whereby it is easy to obtain pure cultures, so that the study of the life-history and functions of the innumerable micro-organisms occurring in nature thus becomes possible.

The authors have isolated from crude sewage, by methods afterwards described, a number of organisms which may serve as typical examples of those usually present in sewage. Some of these have already been described, whilst others are believed to be new organisms. All the organisms described in this paper were isolated from the crude sewage flowing into the sewage works at Acton, London.

The microscopic and macroscopic appearances of the organisms and their pure cultures have been carefully recorded by means of photographs, which give in a permanent form their morphological characters, and the appearance of the plate and tube cultivations in their most characteristic stages of growth. This method of exact illustration the authors consider to be of much importance, as bacteriological descriptions of organisms are frequently of little value owing to the absence of accurate representations of the microscopic preparations and pure cultures.

The experiments hereinafter described were undertaken with the object of studying the reactions of sewage organisms from a chemical point of view, and of gaining information as to the *rationale*, both chemical and bacteriological, of the two marked changes which sewage is liable to undergo, *i.e.*, on the one hand, purification, or the gradual destruction of putrescible matter without the formation of offensively smelling products, and, on the other hand, putrefaction.

For this purpose it was necessary to determine which of the organisms are concerned in the first of these processes, and which in the second, as likewise to gain an insight into the methods by which such changes are effected, for this is little known.

PASTEUR, nearly 30 years ago, in his classical memoir on spontaneous generation, proved that certain forms of microbic life possess the power of rapidly absorbing free oxygen from the atmosphere ('Ann. Chim. Phys.,' vol. 64, 1862, p 78), but as the present methods of obtaining pure cultivations of such organisms were then unknown, he was unable to study the effect of each organism separately as regards the absorption of oxygen.

For all the organisms described in this paper, the authors have determined the absorptive power for free oxygen, when cultivated in a perfectly pure state, and also to which of the organisms free oxygen is a necessity of their activity and growth.

PASTEUR again, in 1863, first showed that certain micro-organisms could carry on their life and growth in a nutrient liquid from which the air had been expelled by boiling ('Comptes Rendus,' vol. 56, 1863, p 416), but it is very doubtful whether he worked with pure cultivations, as they were obtained spontaneously from the dust of the air.

As it is still a point upon which differences of opinion exist as to whether micro-organisms can grow and multiply in absence of the smallest trace of oxygen, each organism has been examined as to its power of growth in a liquid nutrient medium from which every trace of free oxygen, both gaseous and dissolved, has been rigorously excluded.

PASTEUR further pointed out that free access of air was unfavourable to putrefaction, and he believed that it was occasioned by the growth of anaerobic organisms, which were unfavourably affected by the presence of free oxygen, and that the way for their action was prepared by another set of microbes which were aerobic, and used up the oxygen, replacing it by carbonic acid gas. In this relation it will be shown that the anaërobic organisms, producing putrefaction, are themselves (in pure cultivations) capable of absorbing free oxygen with the production of carbonic acid gas, thus preparing the way for their further anaërobic growth.

Various other points of interest have appeared during the progress of the research, which will be more specifically referred to in their proper place without anticipating them here.

The following pages contain detailed descriptions of the experimental methods after which the organisms found in sewage are severally described, with

photographic illustrations, and conclude with a short *résumé* of results and an appendix containing tables and minor details of methods used.

### DESCRIPTION OF EXPERIMENTAL METHODS FOLLOWED

The following methods for the isolation of organisms have been used —

- (1) The method of gelatine plate culture
- (2) A method, to be described later, for the isolation and cultivation of anaerobic organisms
- (3) A method for the isolation of spore-forming organisms.
- (4) The dilution method

All the cultivations, unless otherwise stated, were made at a temperature of 20° to 23° C as nearly as possible.

#### *Plate Cultivations and the Preparation of sterile Gelatine Tubes*

The exact method followed, differing somewhat from the general practice, will be found described in the appendix

#### *Method for the Isolation of Anaerobic Organisms*

The question arose whether the usual method of plate cultivation, carried out, as it is, in contact with air, was equally adapted for the cultivation of anaerobic as well as for aerobic organisms, and it was necessary, in the first place, to ascertain whether any anaerobic organisms existed in the sewage under examination. For this purpose a special form of cultivation flask was devised (fig. 1), suitable not only for mixed cultures, but also for pure cultures, in which the organisms can be grown in an atmosphere of pure hydrogen in absence of every trace of free oxygen

The flask is furnished with a capillary tube *e*, sealed in at *f*, for the purpose of introducing hydrogen. Foreign germs are excluded by a firm plug of sterile wool at *g*.

When it is required to sterilise the flask and its contents before the introduction of pure material or sewage, the fine jet *a* is sealed, and the opening *c*, for the introduction of the culture fluid and organisms, is protected by a sterile plug *d*. The whole is now steamed for 20 minutes on two or three successive days, and is then ready for use

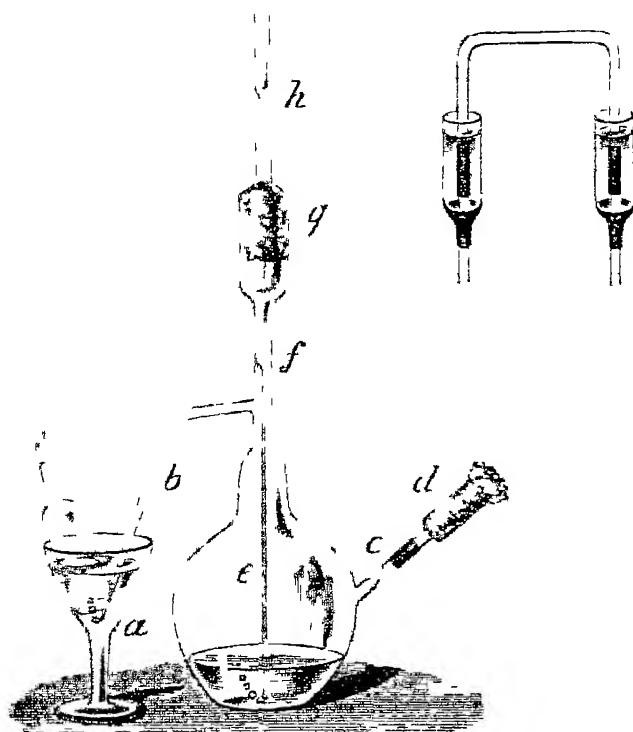
The plug *d* is carefully removed, and a few drops of sewage are introduced by a freshly drawn out capillary pipette, after which the tube is sealed at *c*.

Pure hydrogen is now passed through the liquid (nutrient peptone broth described in the Appendix) by means of the capillary tube *e*, the gas issuing by the broken off end of tube *a*, immersed in water to shut off all communication with the air. The gas is furnished continuously by an apparatus described by the authors in the 'Chemical Society's Transactions' for 1889, p. 561.

After the gas has passed for half an hour, and every trace of oxygen above the

liquid as well as that dissolved\* in it is expelled, the flask is hermetically sealed at *h* and *l*. To prevent internal pressure blowing out the glass on sealing, a little mercury is run into the conical glass until *a* is covered, then a tap in the hydrogen apparatus is opened so as to reduce the pressure, after which the sealing can be accomplished in safety

Fig 1



Hydrogen Flask for Anaerobic cultures

With the object of eliminating all organisms which could not grow in absence of oxygen, a few drops of the turbid and putrescent broth from the first hydrogen flask, after five days' incubation, were sown in a second flask which was filled with hydrogen as before described, and a little material from this second flask was sown in a third similar flask.

By this treatment, not only were all aerobic organisms eliminated, but on making plate cultures of the broth in the usual way in air, one organism alone appeared, and this method may be adopted for its isolation. It is described on p. 644, and closely corresponds to *Proteus vulgaris*.

#### *Method used for the Isolation of Spore-forming Organisms*

A few drops of sewage are introduced into a sterile broth tube by means of a recently drawn out capillary pipette, and the plug is replaced. The tube is now plunged into water at 80° C. for 10 minutes, which treatment kills all the full-grown bacilli, but is not sufficient to kill the spores. The spore-forming organisms may now be isolated by plate culture, either with or without previous incubation of the partially sterilised broth tube.

*The Dilution Method.*—This method may be found useful in isolating certain forms

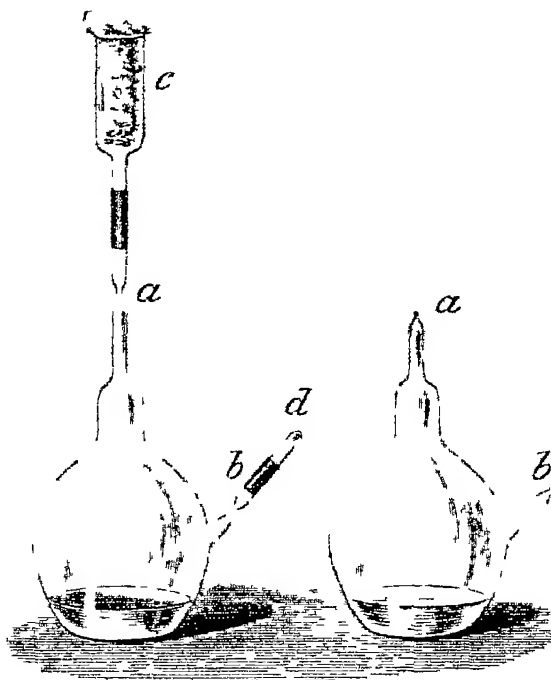
\* The authors have proved this. (See 'Chem. Soc. Trans.,' 1889, p. 554.)

which are not readily separated by plate cultures alone. A few drops of sewage are introduced into a 50 cub centim Chamberland flask filled with sterile water. From this, after mixing, a drop is taken into a second flask of sterile water, and from this, again, into a third containing sterile broth. After a few days incubation the broth is examined microscopically. Usually not more than two distinct organisms appear, which are then easily separated by plate culture. In this manner a new organism (Anaerobic No. 3) was isolated, its extremely characteristic growth in broth pointing it out as a distinct species.

*Reaction of Pure Cultures towards Oxygen.*

For the purpose of studying the reaction towards atmospheric oxygen, the organisms were cultivated in the pure state in sealed flasks containing 25 cub centims of sterile broth and about 250 cub centims of air. A trace of a recent pure culture was used for sowing and in each case the purity of the subsequent growth was tested by plate culture or microscopic observation.

Fig. 2



Flasks for Estimation of Oxygen absorbed

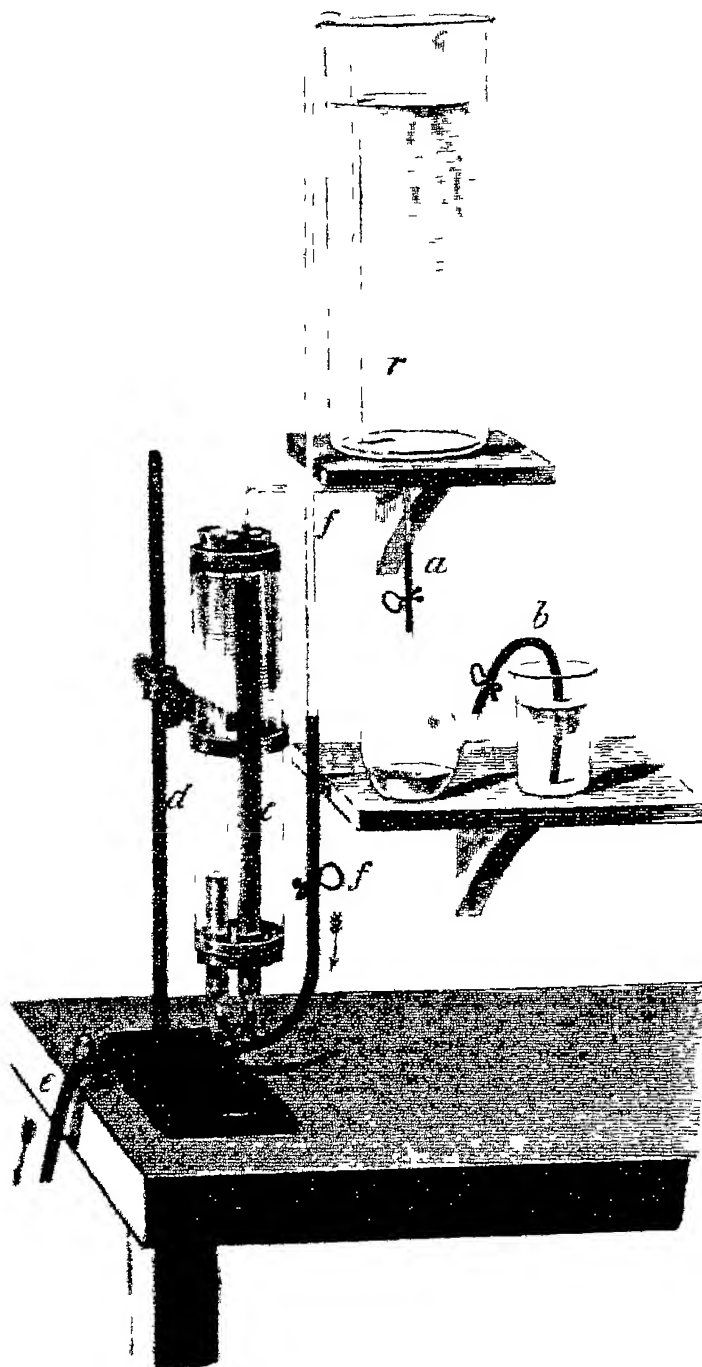
The flasks were furnished with two necks as shown in fig. 2. The lateral neck is plugged by a piece of glass rod *d*, during sterilisation, and after the organisms have been introduced by means of a sterile platinum wire, is sealed off at *b* which afterwards serves for the entrance of water, through the broken end, to replace the gas when it is abstracted for analysis.

The upper neck is connected with a sterile cotton-wool plug *c*, which serves to filter the air entering the flask on cooling after steam sterilisation. This neck when broken also serves for the exit of the gases for analysis, after the incubation of the organisms.

After sowing and sealing off at *a* and *b*, the flasks were incubated at 20°–23° C. for seven days, after which time they were connected by india-rubber tubing filled with

water (fig. 3, *a*) with a Hempel's gas burette and pressure tube surrounded by a water jacket to give a uniform temperature, and by *b* with a beaker of water used for replacing the gas abstracted for analysis.

Fig 3



Method of Estimating Oxygen absorbed.

On breaking the tubes at *a* and *b*, and opening the appropriate pinchcocks, the gas enters the gas-tube *c* previously filled with water, the water flowing out through *e*. It only now remains to connect the Hempel's gas absorption bulbs at *a* instead of the flask, and to force the gas over by water pressure conveyed through *f*.

The carbonic acid and oxygen were absorbed by caustic potash and phosphorus

method of analysis is not relied on for scrupulous exactness, but the results obtained are sufficiently accurate for the purpose aimed at. The amount of

carbonic acid absorbed by the water was neglected, as also was the interchange of dissolved gases

The results of the analyses of the gases are appended in Table I. of Appendix (p 661).

It will be seen that the various organisms exhibit great differences in their absorptive power for free oxygen, some showing the feeblest absorption, whilst others abstracted nearly every trace of oxygen from an atmosphere ten times as large as the culture liquid, during seven days' incubation. For comparison the results are expressed in parts of oxygen remaining and CO<sub>2</sub> produced per 80 volumes of nitrogen, 20 volumes of oxygen representing pure air.

*On the Rate of Absorption of Dissolved Oxygen by Pure Cultures.*

For the purpose of studying the rate at which dissolved oxygen is absorbed from water by the various pure cultures experimented with, tap water, previously sterilised in the steam steriliser and allowed to cool, was fully aerated at the temperature of the incubator 21–22° C as described in a previous paper by the authors ('Chem. Soc Trans,' 1889, p 567). To a Winchester quart bottle of the standard aerated water was added 1 per cent. by volume of broth which had been sown with a minute trace of a pure culture two days previously, and incubated at 20–23° C.

Preliminary experiments with an organism (Aerobic No 4) which absorbed oxygen rapidly showed that in three hours the action had only just commenced, whilst after twenty-one hours all but a trace of oxygen had disappeared

	cub centims
Original volume of oxygen dissolved .	6 04
Oxygen remaining after 3 hours . . .	5 60
„ „ „ 21 hours . . .	·20
Oxygen absorbed, 3 hours . . .	·44
„ „ 21 hours . . .	5·84

The residual oxygen was estimated by the authors' method (*loc. cit.*, p. 562) after an incubation of usually fourteen hours, sometimes longer.

This period of incubation was sufficient, in the case of those organisms which absorb oxygen rapidly, to ensure the disappearance of all but a trace of the oxygen originally dissolved in the liquid. The numerical results will be found in Table II. in the Appendix.

From the results it is seen that all the aerobic organisms which have been shown to absorb oxygen rapidly by the first method also completely absorb the dissolved oxygen in fourteen hours, whereas others which do not absorb oxygen so rapidly by the first method show a corresponding difference here. A blank experiment made with sterile broth showed a slight absorption owing no doubt to slight air contamination of the water during the aëration process, but this effect is so slight as not to influence the conclusions.



*The Necessity of the Presence of Oxygen for the Liquefaction of Gelatine by Anaerobic Organisms*

It was noticed that the only anaerobic organism obtained by a series of broth cultures of crude sewage in hydrogen was one which rapidly liquefied gelatine at the surface only, and it was therefore thought desirable to ascertain whether this surface liquefaction was dependent upon the presence of free oxygen, or whether the organism was capable of liquefying gelatine independently of the presence of oxygen, as it had been found to have the power of growing and multiplying under such conditions.

Accordingly a gelatine culture was made in one of the flasks shown in fig 1, and hydrogen was passed for half-an-hour through the melted gelatine sown with the organism. The flask was then hermetically sealed and incubated at 22° C

In twenty-four hours the previously clear gelatine had become uniformly turbid, but *no liquefaction*, such as takes place in twenty-four hours in a gelatine culture exposed to air, had taken place, and even five days' incubation failed to produce the least liquefaction. After this period, air was admitted, and twenty-four hours afterwards a normal liquefaction over the entire surface was in full progress

Sulphuretted hydrogen was distinctly perceived by smell and proved by its action on lead paper on opening the flask, whilst none is noticed in cultures in air.

Another liquefying anaerobic organism, No 2, was examined in the same way with a precisely similar result, *i.e.*, no liquefaction of the gelatine took place in hydrogen, even after five days' incubation, but liquefaction set in directly on the admission of air and was in full progress over the entire surface of the gelatine (showing that the liquefying action was not produced by subsequent local air contamination) in twenty-four hours after admission of air. In this case, after twenty-four hours' incubation in hydrogen, the gelatine was riddled with small bubbles of gas, but no putrescent smell or sulphuretted hydrogen was perceived on opening the flask, as was perceived with the last organism.

In the case of Aerobic No. 2, the liquefying fluorescing bacillus, a several days' sojourn in pure hydrogen was found not to be fatal, as liquefaction took place over the entire surface twenty-four hours after opening, although the gelatine had remained quite clear in hydrogen. Evidently the organisms had simply remained dormant during the continuance of these eminently adverse conditions, but still *alive* and waiting for more favourable conditions of environment in order to spring into active growth and multiplication. From this it is evident that some at least of the truly aerobic organisms are able to withstand complete deprivation of oxygen without at once succumbing to the adverse conditions.

Again it is shown in Table I. (Appendix) that a larger amount of oxygen is used up, *ceteris paribus*, when gelatine is liquefied than when the growth takes place in broth alone (see Anaerobic No. 1).

*Diminution in the Liquefying Power after long-continued Cultivation in Nutrient Gelatine.*

Whether the characteristic modes of growth on nutrient gelatine would remain constant for each subsequent sub-culture of the organism was a subject of experiment. It was found that some at least of the liquefying bacilli lose to a certain extent their power of rapidly liquefying gelatine. In Anaerobic No. 2 this is more especially marked, and Plate 41, figs. 10, *a* and *b*, show this very clearly. Of these *b* is a recently isolated culture, whilst *a* represents a culture of the same age and incubated in the same gelatine side by side with *b*, but from a culture which has repeatedly passed through the process of sub-culture. Hand-drawn records of the early cultures of *a* are found to be identical with fig. *b*. The liquefied gelatine is uniformly turbid and gives a white deposit at the bottom of the liquefied portion, whilst in *a* the great part of the liquefied gelatine remains clear, the growth collecting into little flocculent masses dotted here and there, whilst the liquefied portion is of much smaller extent for the same age. Both cultures are three days old. Aerobic No. 2 also shows this diminishing power of liquefaction. Plate 41, figs. 11, *a*, *b*, *c*, *d*, show the rate of liquefaction in recently isolated cultures, whilst *e* and *f* show the greatly diminished rate of liquefaction of an old culture. For ages see description of plates.

From these observations it is evident that slight differences in the rate of liquefaction or rapidity of growth which may be observed in cultures which give otherwise identical microscopic and macroscopic appearances, should *not* be relied upon for assuming such differing cultures to be distinct species and naming them by different names accordingly.

It would seem that the previous history and environment of the individual organisms which furnish pure cultures is an important factor in determining the precise nature of the manifestations of its growth in gelatine.

It should be remembered also that non-liquefying organisms are liable to undergo changes of a similar character during extended artificial cultures on gelatine. The two widely differing varieties of non-liquefying fluorescing organisms described in this paper are evidence of such change taking place, as both forms were obtained from a single pure culture tube.

*Resistance of Spores to Heat.*

A few drops of a broth culture of Aerobic No. 4, containing large numbers of spores, were sown into five broth tubes, which were afterwards plunged into water at 80°, 85°, 90°, 95°, and 100° C. for 10 minutes. On incubating the tubes, it was found that the first two tubes alone developed and became crowded with the organism, whilst those heated to 90°, 95°, and 100° C. remained clear and limpid. This is of interest, as the spores of this organism are supposed to be able to withstand a temperature of 100° C.

Further experiments were made by introducing 5 cub. centims. of crude sewage

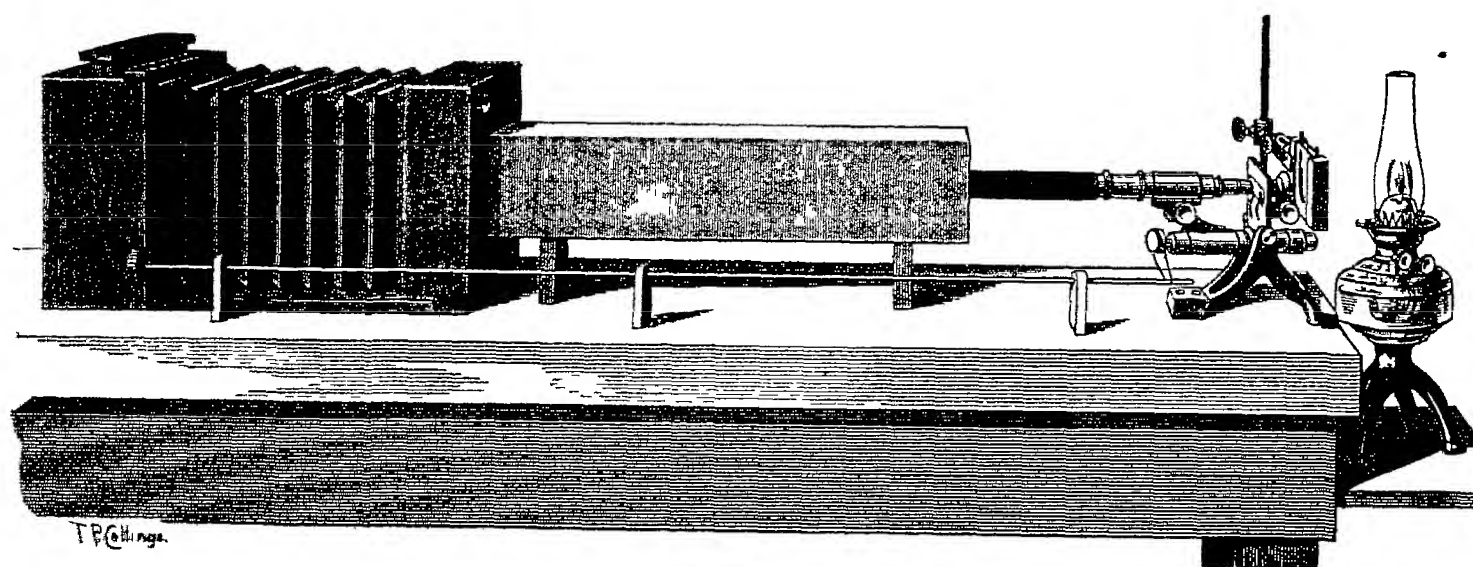
into each of six sterile broth tubes, and placing three in water at  $80^{\circ}\text{C}$  for 10 minutes, whilst the other three were immersed in water in a state of ebullition for the same length of time. The first three became turbid in two days, and yielded three distinct species of organisms, whilst the other three remained perfectly clear for a fortnight, after which time one of the tubes developed a thin film, and afterwards became slightly turbid. The organism causing this was found to be in *Leptothrix* threads of extreme length, these afterwards split up into shorter spore-bearing rods. This organism has not yet been further studied.

### *Method employed for Photographing Bacteria*

The authors have adopted the following method in obtaining the photo-micrographs which accompany this paper. It is very simple, and requires no special apparatus or microscopic accessories.

The arrangement of the apparatus is shown in fig. 4.

Fig. 4



Arrangement for the Photography of Bacteria

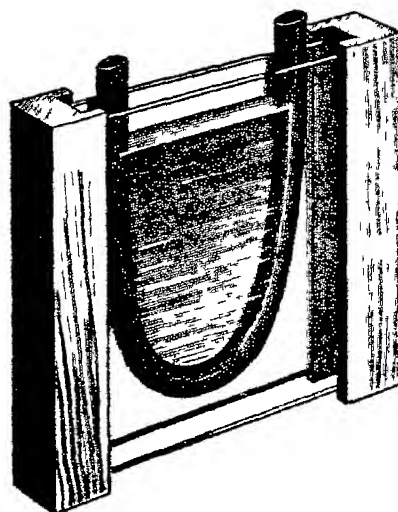
### *The Illumination.*

*Source of Light.*—A common duplex paraffin oil lamp.

*Coloured Screen.*—As the stain employed (methyl violet) transmits actinic rays of light, a coloured screen must be employed, in order to obtain actinic contrast on the sensitive plate. The screen selected was spectroscopically adjusted to the stain employed, the object sought being to illuminate the slide with rays which are totally absorbed by the stain used, and which, where unabsorbed by stain, are sufficiently actinic to give a dense negative with short exposure. A weak solution of potassium bichromate was found to serve the purpose admirably. The absorbent liquid is contained in a thin glass trough (fig. 5) interposed between the lamp and the condenser, made by clamping a semicircle of india-rubber tubing between two plates of glass  $4'' \times 4''$ , by means of two pieces of wood grooved to receive the plates. This

solution absorbs all the blue, indigo, and violet of the spectrum, whilst the stain employed absorbs all the yellow and green. The absorption spectra (fig. 6) of these solutions overlap, so that the stained bacteria appear black on a bright yellow background

Fig. 5



Bichromate Trough for Yellow Light

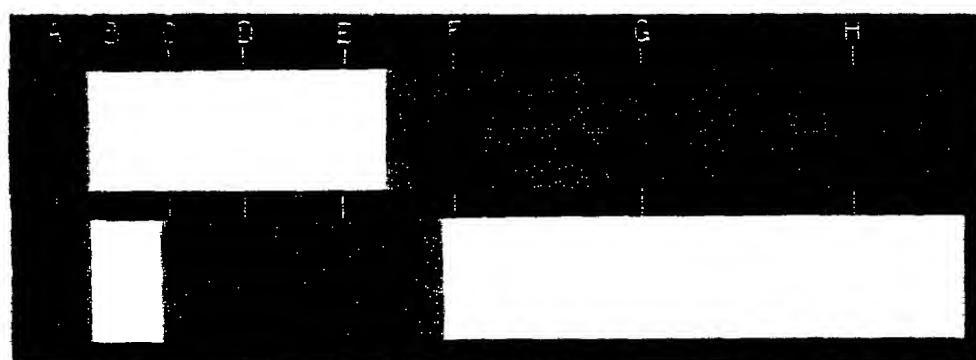
The photographic plates employed must therefore be sensitive to yellow light. Without the interposition of the bichromate screen sufficient actinic light (violet) passes through the stained bacteria to produce a very perceptible action on the photographic plate, thus "fogging" the otherwise sharp and clear outlines of the organisms.

*Condenser*—ABBE's condenser is used, without diaphragm, and is focussed rather farther from the object than for ocular examination.

*Stage*.—A simple clip stage was employed without mechanical accessories.

Fig 6

Absorption spectrum of Potassium Bichromate



Absorption spectrum of Methyl Violet

*The microscopic preparations* were obtained, as a rule, from young pure cultures, thus securing cells full of protoplasm, which stain deeply, an essential for actinic contrast on the photographic plate. Wherever possible cover-glass impressions were taken.\*

\* The authors have extended this mode of preparation to liquids containing mixed or pure cultures with interesting results. Crude sewage, allowed to stand in a covered sterile dish, develops after a while a thin film consisting of various kinds of organisms often aggregated in characteristic pure

*Stain used*—Methyl violet was uniformly employed, and has been found to give very satisfactory results in all cases. In spore-bearing rods the spores are left unstained whilst the rods are stained violet.

*Mounting medium*.—Canada balsam in xylene was uniformly employed. The objections previously entertained to this mounting medium for preparations intended for photography have no weight when the present method of illumination and staining is adopted.

*Lenses*—For the photographs magnified 740 diameters a LEITZ'  $\frac{1}{12}$ th oil immersion was employed. This lens is not usually supposed to be equal to photographic work, yet it may be made to yield very good results. For the photographs magnified 370 diameters a ZEISS' D, and for 50 and 100 a ZEISS' A were used, with the plates at suitable distances from the lens.

No eyepiece was used, nor any lens in the camera, which is connected to the tube of the microscope by a horizontal dark box extension.

*Enlargement* from the original negative has been resorted to only in the case of the photograph (Plate 43, fig. 8) enlarged to 1500 diameters, in order the more clearly to show spore-formation.

*Photographic plates*.—EDWARDS' isochromatic plates have been used throughout.

*Exposure*—For the image thrown by the immersion lens the exposure is about  $1\frac{1}{2}$  minutes, with correspondingly shorter exposures for ZEISS' A and D. The photographs were taken under the disadvantage of vibrations from the vehicular traffic in the street below interfering with the work.

## BACTERIOLOGICAL DESCRIPTION OF THE ANAEROBIC ORGANISMS ISOLATED, *i e.*, THOSE WHICH ARE CAPABLE OF GROWING IN COMPLETE ABSENCE OF FREE OXYGEN

### *Anaerobic Organism No. 1.*

#### *Proteus vulgaris*

This organism was isolated from sewage by a series of broth cultures in hydrogen. The third hydrogen flask, on examination by plate culture, gave this organism only.

*Plate Cultivation*.—Plate 42, fig. 3,  $\times 100$  diams.

In about twenty hours the whole surface of the gelatine plate is covered by a network of swarmers which branch out in all directions. The filmy net-like coating on the surface is too thin and transparent to yield a photograph by ordinary means, the curious structure of the film being almost invisible to the naked eye, so recourse was had to the following method by which the organisms are *stained on the gelatine*

*colonies*. To prepare the impressions a clean sterile cover glass is gently placed on the surface of the liquid by sterile forceps, and withdrawn by tilting up one edge to allow the water to recede without disturbance. The film is dried and stained in the usual way. Plate 43, fig. 3, shows an example of a preparation made in this manner. A pure colony was thus obtained direct from crude sewage!



*plate itself* The plate is first flooded with absolute alcohol, this kills the organisms and fixes them on the dehydrated and hardened gelatine, then an aqueous alcoholic solution of methyl violet is poured on for a few minutes, until the organisms are stained, when the staining fluid is poured off. The plate is now washed once or twice with water and allowed to dry spontaneously. Differential staining takes place, the organisms stain deeply, whilst the gelatine takes but little. The plate which yielded the photograph is permanent, and shows the same field still, exactly as on the day the cultivation was made.

In the depths the threads permeate the gelatine like gnarled rootlets and appear more opaque than the surface swarms. In twenty-four hours, or less if the plate is at all crowded, complete liquefaction ensues. The cultures have an unpleasant sickly odour.

*Stab Cultivations.*—Plate 41, fig. 6, (a) twenty-four hours; (b) forty-eight hours, (c) five days old.

The gelatine becomes liquefied over the entire surface in twenty-four hours, whilst little or no liquefaction has taken place in the needle track. Sometimes the needle track is bristling with rootlet-like projections into the solid gelatine, and shows a very slight incipient liquefaction at the core, and occasionally liquefaction commences at one or two points below the liquefied surface, these appearing as bulbous projections from the central core, filled with turbid liquid having a thick deposit at the bottom. The liquefaction proceeds rather rapidly in a horizontal direction until the whole of the gelatine becomes liquefied, an opaque white deposit remains at the bottom of the culture tube.

*Broth Cultures.*—A very slight and faint film at the surface.

*Microscopic Characters.*—Plate 42, figs. 1 and 2,  $\times 740$  diams.

These are best studied by cover-glass impressions from plate cultures about twenty hours old. The periphery of the colonies (fig. 1) where liquefaction has not commenced, shows long streamers pushing forward in curious convolutions, these, later on, split up into short rods (fig. 2), which are almost exclusively present in the central and older part of the colony.

*Motility.*—The rods are rapidly motile.

*Micrometer Readings.\**—Rods about  $0.6\ \mu$  wide, varying from  $0.4$  to  $0.8\ \mu$ , and of various lengths; the short rods are  $1.4\ \mu$  to  $4.8\ \mu$  long, and all lengths above this may be met with in the long swarms, which often reach  $56\ \mu$  in length.

*Growth in Hydrogen in Gelatine.*—As before described, this organism, when sown in gelatine in an atmosphere of pure hydrogen, renders the medium turbid in twenty-four hours, but *no liquefaction whatever takes place* even after five days. On opening the flask, sulphuretted hydrogen was detected, both by smell and by its reaction with lead paper. Twenty-four hours after opening the flask, the normal surface liquefaction was in full progress, but the smell of sulphuretted hydrogen disappeared.

\* The measurements were made with a LEITZ'  $\frac{1}{36}$  oil immersion, kindly lent by Dr. KLEIN, and a micrometer, for which one division corresponded to  $0.4\ \mu$ .

*Absorption of Atmospheric Oxygen* —Although this organism grows well in entire absence of oxygen, yet the fact that rapid liquefaction of the gelatine surface exposed to air takes place, seems to indicate that oxygen plays an important part in such liquefaction, and this is found to be so on making the experiment in air in a sealed flask.

A larger absorption of oxygen was found to take place in the case where gelatine was used than where broth alone was used. After seven days' incubation the atmosphere was composed as follows —

	Gelatine	Broth
N . . . . .	80 00	80 00
O . . . . .	21	8 21
CO <sub>2</sub> . . . . .	16·43	8·21
Oxygen absorbed . . . . .	<u>19·79</u>	<u>11·79</u>

#### PHOTOGRAPHIC Illustrations.

Plate cultivation, 20 hours old, surface growth stained *in situ*

× 100 diams. . . . . Plate 42, fig 3

Stab cultures (1), 24 hours old, actual size . . . . . Plate 41, fig 6a

„ (2), 48 „ „ . . . . . Plate 41, fig. 6b

„ (3), 5 days old, „ . . . . . Plate 41, fig 6c

Photo-micrograph (1) Edge of colony, showing long rods

× 740 diams . . . . . Plate 42, fig 1

„ „ (2) Showing short rods and two swimmers

× 740 diams. . . . . Plate 42, fig 2

#### *Anaerobic Organism No. 2.*

This organism was isolated from sewage by plate culture and is usually present in large numbers.

*Plate Cultivation.* Plate 40, fig. 1.—The colonies appear to the naked eye in twenty-four hours as microscopic centres of liquefaction fringed by short radiating hair-like projections into the non-liquefied gelatine. In two days the colonies have attained a diameter of 6–8 millims. and appear as liquefied circles with a grey turbidity. No fluorescence is developed.

*Stab Cultivations.* Plate 41, figs. 7, *a*, *b*, and *c*, 10, *a* and *b*—These are very characteristic. In twenty-four hours liquefaction has commenced throughout the needle track, and shows a slightly wider liquefied portion at the surface. In two days the liquefied portion becomes somewhat conical whilst an opaque white deposit collects at the bottom of the needle track. Fig. 7, *a*, shows a tube three days old, whilst *b* and *c* show the same tube at five and seven days old respectively. In about nine to ten



days the whole of the gelatine become liquefied, leaving an opaque white deposit at the bottom of the tube. No film is formed at the surface Fig. 10 shows the diminished power of liquefaction possessed by this organism after repeated sub-cultivation in gelatine The two tubes were inoculated from completely liquefied tubes of the same age, one a recently isolated culture, the other an old culture Both new cultures were in tubes of the same gelatine and were incubated for three days side by side Fig *a* shows the tube from the old culture, liquefaction has not extended very far, the growth is of a flocculent character and a deposit has fallen to the bottom. Fig *b*, from the recent culture, shows a thickly turbid liquid, liquefaction has proceeded much more rapidly than in fig. *a*

*Broth Cultures*—No film is formed at the surface

*Agar Agar*—Creamy-white moist growth which does not extend far from the central line

*Potato*—Grows well on potato, giving a brownish-white moist growth

*Microscopic Characters* Plate 42, figs 4 and 5,  $\times 740$  diams—The early cultures of this organism showed mainly short rods with occasional very long rods (fig 4). In old cultures, after repeated sub-cultures in gelatine, not only does the organism show a diminished power of liquefying gelatine but the microscopic characters also become greatly changed Involution forms of all kinds appear, distinctly celled chains of rods of varying length and thickness, extremely long tapering rods often with club-shaped ends, rods of very various lengths singly and in short chains of three or more (fig. 5)

*Motility*—The rods are rapidly motile.

*Micrometer Readings.*—The rods are at first from  $0.4\mu$  to  $0.6\mu$  wide, and of variable length from bacillo-cocci to very long rods and chains.

*Growth in Hydrogen in Gelatine*—Sown in gelatine, in an atmosphere of pure hydrogen, the gelatine becomes turbid after twenty-four hours' incubation, and also riddled with minute bubbles of gas, but *no liquefaction whatever* takes place even after five days' incubation in hydrogen; twenty-four hours after opening the flask, however, the whole surface becomes liquefied under the influence of the oxygen which is admitted In broth, in hydrogen, the organism grows as very short rods, scarcely longer than broad No objectionable odour or sulphuretted hydrogen is perceived, either before or after access of air

*Absorption of Atmospheric Oxygen.*—A slight absorption only takes place. After seven days' incubation of 25 cub. centims of infected broth in 250 cub. centims. of air, the atmosphere possessed the following composition.—

N . . . . .	80.00
O . . . . .	17.60
CO <sub>2</sub> . . . . .	3.80
Oxygen absorbed . . . . .	2.40

## PHOTOGRAPHIC Illustrations

Plate cultivation	. 2 days old, actual size	Plate 40, fig	1
Stab cultures (rather old sub-culture) (1), 3	„ „	Plate 41, fig	7a
„ „ „ (2), 5	„ „	Plate 41, fig	7b
„ „ „ (3), 7	„ „	Plate 41, fig	7c
„ „ „ (4), Old culture	} 3 days {	Plate 41, fig	10a
„ „ „ (5), New culture		Plate 41, fig	10b
Photo-micrograph, new culture, short rods $\times 740$ diams	.	Plate 42, fig	4
„ „ old „ involution forms $\times 740$ diams		Plate 42, fig	5

*Anaerobic Organism No 3**Streptococcus mirabilis*

This organism was isolated from sewage by the dilution method, and appeared in a broth flask, accompanied by a bacillus, from which it was separated by plate culture

*Plate Cultivation* Plate 40, fig 2,  $\times 50$  diams—This organism grows badly in gelatine, and even after four days the colonies appear in the depths of the gelatine as mere microscopic dots or gnarled and convoluted thread-like masses. Some surface colonies, especially in the early cultures, show an exceedingly faint and transparent expansion about 2 millims. in diameter, this examined microscopically with a low power is seen to consist of a mass of fine long threads, sometimes throwing out processes into the surrounding gelatine. These colonies are not amenable to cover-glass impressions, as they obstinately refuse to leave the gelatine. Fig 2 shows a photograph ( $\times 50$  diams) of a preparation of a colony obtained as follows—The gelatine plate was flooded with dilute nitric acid, which dissolved the gelatine and set the colony free, this was then gently floated on a cover-glass, where it was left stranded, the colony was then washed and dried and stained in the usual manner. Plate 42, fig. 8, shows a small portion of the edge of this colony  $\times 370$  diams, and well illustrates the loops which spring out into the adjacent gelatine. No liquefaction of the gelatine takes place even in old cultivations, and growth apparently ceases after the first five or six days.

*Streak Cultures on Gelatine* Plate 41, fig. 1—An exceedingly faint and transparent film, almost invisible to the naked eye, which grows for a few days, attaining a diameter of about 3–5 millims., at which point further growth ceases. A very characteristic culture is obtained in the following manner—a streak culture on gelatine is made, and when seven days old the tube is filled up with sterile broth, submerging the gelatine. The streak on the gelatine soon begins to throw out fluffy

loops of threads into the broth. The figure (fig. 1) shows such a culture, grown seven days in gelatine, and a further seven days in the broth. The growth stands out from the gelatine into the broth as a fine fluffy mass, resembling delicate cotton wool; the gelatine is shown on the right, whilst the broth on the left, above the fluffy growth, remains perfectly clear and limpid.

*Broth Cultures*—These are very characteristic. In forty-eight hours nearly the maximum growth has taken place: a fine mass resembling delicate cotton-wool rests at the bottom of the test-tube, or is carried upwards in delicate festooned threads by the convection currents in the liquid. When the tube is taken out of the incubator, and convection currents cease, the festooned threads fall to the bottom, leaving the broth above perfectly clear and limpid. It is a characteristic of this organism, owing to its growing in such interminably long threads, that the broth in which it grows is not rendered turbid in the least.

*Agar Agar*.—The growth on this medium is very similar to that on gelatine, being a very faint slight expansion.

*Potato*—Inappreciable growth.

*Microscopic Characters*. Plate 42, figs. 7 and 8.—Streptococci in chains of extreme length, rarely splitting off into short threads, hence the non-turbidity of the broth cultures.

*Motility*—The organism is non-motile.

*Micrometer Readings*—The chains are about  $0.4 \mu$  thick, and the individual cells vary from  $0.4 \mu$  in the single cells to about  $1.2 \mu$  in the diplococci undergoing fission.

*Growth in Broth in Hydrogen*—The organism grows quite as readily in pure hydrogen as in air, and with the same characteristic appearance.

*Absorption of Atmospheric Oxygen*.—After seven days the absorption of oxygen is almost *nil*, and is the smallest of any result obtained. The atmosphere gave on analysis the following numbers:—

N	80.00
O . . . . .	19.50
CO <sub>2</sub> . . . . .	30
Oxygen absorbed . . . . .	50

#### PHOTOGRAPHIC ILLUSTRATIONS.

Colony 7 days old, preparation by nitric acid method described,

× 50 diams . . . . . Plate 40, fig. 2.

Streak culture, 7 days on gelatine and 7 days in broth . . . Plate 41, fig. 1.

Photo-micrograph, small portion of edge of above colony, × 370 . . . Plate 42, fig. 8.

„ „ preparation of broth culture 24 hours old,

× 740 . . . . . Plate 42, fig. 7.

*Anaerobic Organism No 4.**Bacillus opalescens*

This organism was isolated from sewage direct by plate culture, it occurs plentifully in the sewage experimented with

*Plate Cultivation* Plate 40, fig 3 —The colonies are easily visible as small faint expansions after twenty-four hours' incubation, diameter 1–2 millims. In two days they are very characteristic, appearing as a thin opalescent film, about 8 millims. diameter, with an irregular wavy edge of extreme thinness. The colonies are admirably adapted for cover-glass impressions, the edge showing a single layer of well-defined rods. No liquefaction takes place even in old cultures. No fluorescence is produced. The colonies seem to have an aversion to coalesce with each other, the edge of a colony near its neighbour grows less quickly, whilst the edges which have a free course shoot out more quickly into the unoccupied space.

*Streak Cultures.*—Plate 41, fig 2, shows a streak two days old. The gauzy and irregular margins are well seen, the film is of an opalescent character.

*Stab Cultures.*—The growth is confined to the surface, which is covered completely in three or four days, when the growth ceases. No liquefaction whatever takes place.

*Agar Agar.*—A creamy white moist growth which does not extend far from the central line.

*Potato* —Grows well on potato, giving a brownish-white slimy growth.

*Microscopic Characters* Plate 43, figs 1 and 2.—These are best studied by cover-glass impressions. The delicate edges of the colonies are seen to be formed by a single layer of well-defined rods of uniform length, these divide in the older stages into short rods, and even cocci. The photographs show all the forms from one cover-glass impression. Fig. 1 shows the long rods from the edge of a colony, whilst fig 2 shows the uppermost layer of organisms from the centre of the colony.

*Motility* —This organism is motile.

*Micrometer Readings.*—The long rods measure about  $0.5 \mu$  wide and  $4 \mu$  long, whilst the older forms may be cocci  $0.4 \mu$  in diameter.

*Growth in Hydrogen* —The broth becomes turbid in twenty-four hours, but the growth is not so copious as in air. After a few days a white sediment falls to the bottom. Here the cocci forms predominate.

*Absorption of Atmospheric Oxygen* —The absorption of oxygen by this organism is not very rapid. After seven days the atmosphere possessed the following composition —

N . . .	80 0
O . . . . .	13 3
CO <sub>2</sub> . . . . .	6 3
Oxygen absorbed . . . . .	6 7

## PHOTOGRAPHIC Illustrations

Colonies on gelatine, two days old	.	Plate 40, fig 3
Streak culture on gelatine two days old	.	Plate 41, fig 2
Photo-micrograph (1) Long rods, edge of colony, $\times 740$ diams		Plate 43, fig 1.
„ „ (2) Short rods and cocci, centre of colony, $\times 740$ diams	.	Plate 43, fig 2.

*Anaerobic Organism No 5.*

This organism was isolated from sewage-infected broth incubated in hydrogen, by the method for isolating spore-forming organisms

*Plate Cultivation.*—The colonies appear on the second day as tiny translucent droplets, they never exceed 2 to 3 millims in diameter. when further growth ceases Owing to its very difficult growth on gelatine this organism has not yet been completely examined

*Streak Cultivation* —A faint translucent and very narrow streak, about 1–2 millims wide, develops after two days, but no further growth takes place No liquefaction of the gelatine takes place

*Broth Cultures* —These also grow badly.

*Microscopic Characters* —Plate 42, fig 6, shows a cover-glass impression from an isolated colony. This has been so treated in the heating and washing, that only the first layer of organisms has been fixed on the cover-glass, the lower layers, which would otherwise make the preparation quite opaque, have all been washed away from the preparation without disturbing the first layer. The wave-like arrangement of the rods is very marked

*Micrometer Readings.*—The rods are 0.5 to 0.8  $\mu$  wide and 1.8 to 5.2  $\mu$  long

Plate 40, fig 5, shows this cover-glass impression viewed in its entirety by a low power, with dark ground illumination. The mottled appearance is very curious It is caused by the arrangement in different directions of the single layer of rods, whereby, in one direction, light is able to pass, whereas, in the other it is not.

## PHOTOGRAPHIC Illustrations.

Photo-micrographs, cover-glass impression, three days old, dark ground illumination, showing mottled appearance, $\times 50$	.	Plate 40, fig. 5.
Ditto, more highly magnified, $\times 370$	.	Plate 42, fig 5.

BACTERIOLOGICAL DESCRIPTION OF AEROBIC ORGANISMS ISOLATED, *i e*, THOSE WHICH ARE INCAPABLE OF GROWING EXCEPT IN PRESENCE OF FREE OXYGEN

*Aerobic Organism No 1.*

*Bacillus fluorescens non-liquefaciens (A).*

This organism was isolated from sewage by plate culture

*Plate Cultivation* Plate 40, fig 7a —The colonies are easily visible to the naked eye as small transparent expansions on the surface of the gelatine after twenty-four hours' incubation. In two days the surface colonies have attained a diameter of 3-3.5 millims., the edges are very delicately thin and irregular, whilst the central and older portion is thicker and of a slightly grey colour. These colonies are admirably adapted for the preparation of cover-glass impressions, the margins showing a delicate single layer of well-defined rods.

On the second day the colonies are surrounded by a broad halo of beautiful bluish-green fluorescence. After three or four days' incubation, softening and incipient liquefaction of the gelatine commences, this proceeds very slowly and not at all if grown at the ordinary temperature. In old cultures the bluish-green fluorescence fades, and is replaced by a brown colour.

*Streak Cultivations, Gelatine* Plate 41, fig 4a —The streak grows rapidly for two or three days, after which time the growth proceeds but slowly. Fluorescence is very marked after two days' growth. The photograph well shows the gauzy irregular margin of the growth and the incipient softening of the gelatine in the central portion.

*Broth Cultures* —A slight film is formed at the surface and the broth is tinged a fluorescent green.

*Agar Agar.* —A greyish-white growth which does not extend far from the central line. The whole of the agar agar is tinged a fluorescent green.

*Potato.* —A creamy white growth which soon turns brown, and does not extend over the entire surface.

*Microscopic Characters.* Plate 43, fig 6. —Thin motile rods, longer and slightly thicker in the early stages (edge of colony), than in the later ones. This organism does not form chains, and very rarely long rods, and is identical in cover-glass impressions with Plate 43, fig. 6.

*Motility.* —The rods are motile.

*Growth in Hydrogen.* —This organism refuses to grow in an atmosphere deprived of oxygen.

*Absorption of Atmospheric Oxygen* —This organism is a greedy absorber of gaseous oxygen. In one experiment a 25 cubic centims. broth culture sealed up in 250 cubic centims. of air, deprived the atmosphere of all but a trace of oxygen during seven days' incubation. The analysis of the gases gave the following —

N .	80 00
O	. 14
CO <sub>2</sub>	. 12 04

In another experiment made side by side with the next-described organism the results were, for seven days —

N	80 0
O	7 9
CO <sub>2</sub>	8 6

The diminished rate of absorption is not easily explainable except by the fact that the second experiment was sown from an older and perhaps weaker culture

### PHOTOGRAPHIC Illustrations

Plate cultivation, 2 days old, actual size	. Plate 40, fig 7 <i>a</i>
Streak cultivation, 3 days old	. Plate 41, fig 4 <i>''</i> .
Photo-micrograph, cover-glass impression, edge of colony, × 740 (identical with)	. . . Plate 43, fig 6

### *Acrobic Organism No 1A*

#### *Bacillus fluorescens non-liquefaciens* (B)

This organism, evidently a variety of the one last described, was isolated from a culture of that organism which had repeatedly passed through plate culture, and which, therefore, was undoubtedly pure. On making a fresh plate cultivation from a streak tube it yielded two varieties of fluorescent colonies, each of which retained its character in subsequent cultures. The organisms are strikingly alike in their fluorescent power, but distinct in their gelatine cultures and in microscopic preparations. The authors believe that here some subtle change has taken place in a portion of a pure culture by which the character of the organism is altered, thus giving rise to two varieties. This variety has also been isolated direct from sewage.

*Plate Cultivation.* Plate 40, fig 7*b*.—In two days, plates side by side with those of the first variety *grew less quickly*, the colonies not exceeding 2 millims. in diameter; the outline of these is quite sharp and *circular*, the edges being much thicker in contrast to the first variety with its gauzy margins and irregular outline. The colonies are thicker and whiter in colour, and show the same fluorescence as the first variety.

*Streak Cultivation.* Plate 41, fig. 4*b* —These show a marked contrast to 4*a*, as is seen very well in the photograph. Incipient liquefaction does not commence until the fifth day's incubation, whilst in 4*a* it is present on the third day.

*Stab Cultivations.*—The surface growth is like the colonies, a circular head; there



is little growth in the needle track; the fluorescence extends throughout the whole of the gelatine after about a week's incubation

*Agar Agar and Potatoes*—Similar to the preceding organism

*Microscopic Characters.* Plate 43, fig 3—Here the difference is marked, this variety is encapsuled, whilst the first variety is not

*Growth in Hydrogen.*—This organism refuses to grow in an atmosphere deprived of oxygen

*Absorption of Atmospheric Oxygen*—The experiment made side by side with the one last named gave the following numbers —

N	. . .	80 0
O	. . .	4·9
CO <sub>2</sub>	. . .	10 1

#### PHOTOGRAPHIC Illustrations.

Plate cultivation, 2 days old, actual size	Plate 40, fig 7b
Streak cultivation, 3 days old, actual size.	Plate 41, fig 4b
Photo-micrograph, encapsuled rods direct from sewage (see p. 643, footnote) × 740 diams . . .	Plate 43, fig 3

It was considered desirable to expose crude sewage to a large surface of air and allow the natural changes to go on for some time, in order to ascertain the nature of the organisms which would thrive under those conditions. For this purpose crude sewage was introduced into a sterilised and covered Petri's dish and allowed to remain for two months. After this length of time cover-glass impressions and plate cultures were made from the liquid, when it was found that the former showed plentiful pure colonies of encapsuled rods.

Plate 43, fig 3, shows a photograph of such a colony; the plate cultivations too yielded the non-liquefying fluorescent colonies and encapsuled rods described above

This organism and the preceding closely correspond to the organisms isolated by Dr. KLEIN from poisonous veal and pork.

#### *Aerobic Organism No 2* *Bacillus fluorescens liquefaciens.*

This organism was isolated from sewage by plate culture direct, it occurs plentifully in sewage.

*Plate Cultivation.* Plate 40, figs. 10 a and b—The colonies develop with extreme rapidity. In twenty-four hours they appear as slightly fluorescent liquefied circles 2-3 millims. in diameter, and grow so rapidly as to cover 4-5 millims in another three

hours It is interesting to observe that the colonies submerged in the gelatine appear as mere dots during this extremely rapid liquefaction taking place in the surface colonies, showing the accelerative effects of a copious supply of oxygen. A successful plate must contain very few colonies or complete liquefaction of the whole of the gelatine soon takes place.

*Stab Cultivations* Plate 41, figs 11, *a* to *d*—The liquefaction stretches half across the surface of the gelatine in twenty-four hours, forming a curved turbid portion beneath (fig. *a*). In twenty-seven and a half hours the liquefaction has extended almost across the surface, whilst the needle track in the depths remains undeveloped (fig. *b*). Figs *c* and *d* show the further course of the liquefaction. After two or three days the liquid shows a greenish fluorescence which becomes more marked in old cultures.

*Microscopic Characters*—Short motile rods corresponding to Plate 42, fig. 4, length variable, width  $0.4\ \mu$  to  $0.7\ \mu$ .

*Absorption of Atmospheric Oxygen*.—This organism absorbs oxygen rapidly; in one experiment the growth abstracted nearly all the oxygen in three days, and in another of seven days' incubation the merest trace of oxygen was found. In a later series of experiments, however, the absorption was not so rapid. The following are the numbers obtained—

	(1)	(2)	(3)	(4)
	3 days	7 days.	3 days.	7 days
N .	80.0	80.0	80.0	80.0
O	1.0	0.0	12.8	4.6
CO <sub>2</sub> . .	10.7	12.7	5.4	11.4

*Growth in Hydrogen*—No growth takes place in gelatine, nevertheless, the organisms retain their vitality for some days at least, and normal liquefaction proceeds on admitting air to the flask.

#### PHOTOGRAPHIC Illustrations.

Plate cultivations, 24 hours old, actual size	Plate 40, fig. 10 <i>a</i>
„ 27 „ „ „ „	Plate 40, fig. 10 <i>b</i>
Stab cultivations, 24 „ „ „ „	Plate 41, fig. 11 <i>a</i>
„ 27½ „ „ „ „	fig. 11 <i>b</i>
„ 48 „ „ „ „	fig. 11 <i>c</i>
„ 4 days old „ „ „ „	fig. 11 <i>d</i>
„ old cultures, 3 days old.	fig. 11 <i>e</i>
„ „ 7 „ „ „ „	fig. 11 <i>f</i>
Photo-micrograph $\times 740$ diams. (identical with)	Plate 42, fig. 4

*Aerobic Organism No. 3.**Bacillus subtilis*

This organism was isolated from sewage by the method described for isolating spore-forming organisms. A broth tube containing 2 cubic centims of crude sewage was placed in water at 80° C for ten minutes, and incubated for two days. After this period of incubation the broth swarmed with this organism, which was obtained in the pure state from this material by plate cultivation.

*Plate Cultivation* Plate 40, fig 9 —The colonies begin to appear as liquefying dots in twenty-four hours, on the second day the surface colonies have attained a diameter of 14–16 millims. They appear as liquefied circles, covered in the central portion by a more or less perfect film. Microscopically, the edges of the colonies exhibit short streamer-like projections into the non-liquefied gelatine, and the colony appears crowded with dark dots, which vanish and reappear, probably due to the rods presenting an end and side view alternately whilst moving about in the liquid. No objectionable odour is perceived.

*Stab Cultivations* Plate 41, fig 8, *a* and *b* —The liquefaction of the gelatine begins as a hemispherical turbid portion at the point of entrance of the needle. Fig 8*a* shows a tube twenty-four hours old. On the second day, the liquefaction extends across the tube and for several millimetres downwards, whilst the needle track below has become liquefied and has widened out. A white firm film is formed on the surface consisting of matted threads of the organism in a non-motile condition. After about seven days this film is crowded with spores.

The whole of the gelatine becomes liquefied after 7–10 days when a somewhat flocculent deposit is formed at the bottom of the tube, whilst the liquid beneath the film becomes comparatively clear.

*Broth Cultures.*—In these a firm film forms on the surface in three or four days, and this falls to the bottom when shaken.

*Microscopic Characters* Plate 43, figs 7 and 8.—Bacilli singly in twos, threes, and short chains, which sometimes may consist of more than a dozen elements. Fig. 7 is a photograph of a cover-glass impression, from the fourteen days old broth which had been poured out into a sterile dish, from the sealed flask used for the determination of the absorption of oxygen. The preparation was made the day after pouring into the dish, and curiously enough shows mainly long chains. The short chains, however, consisting of but two or three elements, are more characteristic of the gelatine cultures. Spore formation is observed after seven days' incubation, and Plate 43, fig. 8, shows an enlargement  $\times 1500$  diameters, taken from a photograph  $\times 740$  diameters. The spores were not stained in the preparation, and come out white in the photograph.

*Motility.*—In the fresh state the rods are motile, whilst the zooglea film is a mass of interlacing non-motile rods, which soon forms spores.

*Micrometer Readings*—Rods  $0.5\ \mu$  to  $1\ \mu$  wide and  $3\ \mu$  to  $5\ \mu$  long. The spores measure about  $0.8\ \mu$  wide and  $1.2\ \mu$  long, and are often thicker than the rods bearing them.

*Growth in Hydrogen*—No development takes place, but a fourteen days' deprivation of oxygen was found not to be fatal, as on the second day after opening to the air the liquid swarmed with the rapidly motile rods.

*Absorption of Atmospheric Oxygen*—Rapid absorption of oxygen takes place. After seven days and fourteen days respectively, two experiments gave.—

Seven days.		Fourteen days	
N	80.0	N	80.0
O	9.0	O	0.8
CO <sub>2</sub>	8.8	CO <sub>2</sub>	14.1
Oxygen absorbed	11.0	Oxygen absorbed	19.2

*Resistance of the Spores to Heat*—From a completely liquefied gelatine tube, crowded with spores, sowings were made in five tubes of sterile broth, and the tubes afterwards placed for ten minutes in water at  $80^\circ$ ,  $85^\circ$ ,  $90^\circ$ ,  $95^\circ$ , and  $100^\circ$  C, respectively. They were then allowed to cool and placed in the incubator. After two days, the  $80^\circ$  and  $85^\circ$  tubes became turbid, and afterwards developed the characteristic film and rods of the organism. Spore-formation also took place. The  $90^\circ$ ,  $95^\circ$ , and  $100^\circ$  C tubes all remained perfectly clear and limpid.

#### PHOTOGRAPHIC Illustrations.

Plate cultivation, 2 days old, actual size	Plate 40, fig. 9
Stab cultures, 24 hours old	Plate 41, fig. 8a
„ 2 days „	Plate 41, fig. 8b
Photo-micrographs, <i>Leptothrix</i> threads, $\times 710$ diams	Plate 43, fig. 7
Enlargement, spore-bearing rods, $\times 1500$ diams.	Plate 43, fig. 8

#### *Aerobic Organism No. 4*

##### *Bacillus violaceus.*

This organism was isolated from sewage by plate cultivation.

*Plate Cultivations* Plate 40, fig. 8.—The colonies closely resemble those of Anaerobic Organism No. 4. They grow, however, rather more slowly, and the films are thicker and more opaque, and the edges are not so delicate. After five or six days' growth the colonies assume a deep violet colour, and in this manner they are sharply distinguished from the organism mentioned.

*Streak Culture.* Plate 41, fig. 3.—The photograph shows the appearance of a streak

culture, three days old; in this, the violet colour has not yet appeared, but the growth is yellowish-white. After five or six days the colour begins to turn violet, and soon afterwards liquefaction of the gelatine sets in, and ultimately involves the whole of the gelatine, whilst a rather thick deposit of a dirty violet colour collects at the bottom of the tube.

*Broth Cultures*—A thick film of a dirty violet colour is formed, whilst the liquid is coloured brown.

*Agar Agar*—A grey-white moist growth, which gradually assumes a bluish-violet colour, which is especially marked at the surface of the liquid collected at the bottom of the tube. The deposit at the bottom of the liquid is white.

*Potato*.—A thick moist brown expansion with old cultivation.

*Microscopic Characters* Plate 43, fig 6.—Bacilli corresponding microscopically to Aerobic No 1. Fig 6 is from a photograph of a cover-glass impression showing the edge of a colony.

*Motility*.—The organism examined in the living state is motile.

*Growth in Hydrogen*.—No growth takes place.

*Absorption of Oxygen*.—Like all the film-forming organisms, this absorbs oxygen rapidly. After seven days the atmosphere was almost deprived of oxygen.

N . . . . .	80 00
O . . . . .	14
CO <sub>2</sub> . . . . .	12·06
Oxygen absorbed . . . . .	19 86

#### PHOTOGRAPHIC Illustrations

Plate cultivation, 2 days old, actual size . . . . .	Plate 40, fig 8
Streak cultivation, 3 days old, actual size . . . . .	Plate 41, fig. 3
Photo-micrograph, edge of colony, × 740 diams	Plate 43, fig. 6.

#### *Aerobic Organism No 5.*

##### *Streptococcus ureæ*

This organism was isolated from sewage direct by plate culture.

*Plate Cultivation*. Plate 40, fig. 6.—The colonies begin to appear on the second day as minute dots, on the third day the surface colonies have acquired a diameter of 2 millims., and on the fifth day (fig. 6) the increase is only to 3 millims., from this point the growth proceeds very slowly. No liquefaction takes place even in old cultures. In contour the colonies are well-defined circles, and appear as shining drops of wax of an opaque yellowish-white colour.

*Streak Cultivations*.—Plate 41, fig. 5, shows a cultivation three days old. After this

point the further growth takes place very slowly, giving a straight waxy streak. No liquefaction ever takes place.

*Stab Cultures* —A well-defined circular head, corresponding to the appearance on plates, develops at the point of entrance of the needle. Little growth is noticed in the needle track.

*Agar Agar* —A grey-white moist growth, which does not extend far from the central line.

*Potato* —A creamy-yellow thick growth.

*Microscopic Characters.* Plate 43, fig 4 —This organism is apparently a streptococcus, growing in short chains, and in ones and twos. The preparation is from a young and vigorously growing cultivation, and shows all the transition stages from the true streptococci through chains of oval and then bacilli-like cells, which subsequently split off into cocci.

*Motility* —This organism is non-motile.

*Micrometer Readings* —The cells are  $0.8\ \mu$  to  $1.2\ \mu$  wide, and  $0.8\ \mu$  to  $2.4\ \mu$  long, according to stage.

*Growth in Hydrogen* —No growth was observed.

*Absorption of Atmospheric Oxygen* —The growth in broth is not so rapid and the turbidity not so dense as in the case of other organisms, and the absorption of oxygen takes place but slowly. After seven days the atmosphere was composed as follows:—

N	80.0
O . . . . .	14.0
CO <sub>2</sub>	3.6
Oxygen absorbed . . . . .	6.0

#### PHOTOGRAPHIC Illustrations.

Plate cultivation, 5 days old, actual size. . . . .	Plate 40, fig 6.
Streak cultivation, 3 days old, actual size . . . . .	Plate 41, fig 5
Photo-micrograph, showing all the transition stages in streptococci, $\times 740$ diams . . . . .	Plate 43, fig 4.

#### *Aerobic Organism No. 6.*

##### Micrococcus

This organism was isolated by plate cultivation from sewage direct. It is interesting to note that it is the only micrococcus met with.

*Plate Cultivation.* Plate 40, fig. 4.—This organism grows very slowly, the colonies appearing as minute dots on the second day. The first crowded plate is viscid and possesses a sickly odour. On the fifth day the colonies have only advanced to 2 millims diameter. Microscopically, the colonies appear as dark well-defined spheres. Incipient liquefaction commences about the fifth day and proceeds but slowly, the

gelatine only becomes viscid and not really liquid. The colour of the growth is a pale yellowish-brown.

*Stab Cultivations*.—Plate 41, figs 9, *a* and *b*—There is but little growth in three days, when a slight viscid depression is formed at the entrance of the needle, but little growth takes place in the needle track. The photographs show stab cultivations seven and fourteen days old respectively.

*Agar Agar*.—A slight yellow growth, showing a tendency to collect in dioplets.

*Potato*.—A very poor growth of a dry yellow crumpled nature.

*Microscopic Characters*.—Cocci  $0.5\ \mu$  to  $0.8\ \mu$  diam, which exhibit only the usual vibratory movements.

*Absorption of Atmospheric Oxygen*.—The absorption is very slow, corresponding to that given by Anaerobic No. 2. After seven days' incubation the results were—

N	.	80.0
O	.	17.6
CO <sub>2</sub>		5.8
Oxygen absorbed	.	2.4

#### PHOTOGRAPHIC Illustrations

Plate cultivation, 5 days old, actual size	Plate 40, fig 4
Stab cultivations, 7 „ „	Plate 41, fig 9 <i>a</i>
„ 14 „ „	Plate 41, fig 9 <i>b</i>

#### Résumé

Of the twelve organisms studied, five are capable of growing in complete absence of free oxygen, whilst to the other seven free oxygen is a necessity.

Of the five organisms which can grow without free oxygen, one only, the first one, shows a vigorous absorption of this gas, and this is the one which gives rise to offensive decomposition of the nutrient material.

Of the seven organisms to which free oxygen is a necessity, five are rapid absorbers of that gas, and all of them form films of a more or less marked character when cultivated in nutrient broth, and it would seem that the chemical signification of such film-forming at the surface, is, that the organisms require and absorb a large amount of free oxygen. These organisms therefore may be regarded as a means of slow combustion and destruction of the organic matter of sewage.

The other two organisms which do not form films absorb oxygen much less rapidly.

Of the twelve organisms, four rapidly liquefy gelatine, and of these two are anaerobic and two aerobic. Four liquefy gelatine slightly after lapse of several days' cultivation. These are all aerobic. The remaining four do not liquefy the gelatine at all, even in old cultivations. Nine of the organisms belong to the class of Bacilli, whilst two are Streptococci and one a Micrococcus.



## APPENDIX.

TABLE I —Showing the Absorption of Oxygen from the Atmosphere of Sealed Flasks (fig 2), containing 25 cub centims of Nutrient Broth, and 250 cub centims of Air, and sown with Traces of Pure Cultures of the Organisms Temperature of Incubation, 20°–23° C

*A Anaerobic Organisms*

Organism	No 1 (Broth)	No 1 (Gelatine)	No 2	No 3 *	No 4
Duration of incubation	7 days	7 days	7 days	7 days	7 days
Composition of residual atmosphere	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$
Oxygen absorbed per 80 parts nitrogen	11.89	19.79	2.4	0.5	6.7

*B. Aerobic Organisms*

Organism	No 1	No. 1	No 1A	No 2	No 2	No 2	No 2
Duration of incubation	7 days	7 days	7 days	3 days	7 days	3 days	7 days
Composition of residual atmosphere	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$
Oxygen absorbed per 80 parts nitrogen	19.86	12.1	15.1	19.0	20.0	7.2	15.4

Organism	No 3	No 3	No 4	No 5	No 6
Duration of incubation	7 days	14 days	7 days	7 days	7 days
Composition of residual atmosphere	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$	$\left\{ \begin{array}{l} \text{N} \\ \text{O} \\ \text{CO}_2 \end{array} \right.$
Oxygen absorbed per 80 parts nitrogen	11.0	19.2	19.86	6.0	2.4

\* This result may be taken as a blank experiment to show that no appreciable absorption takes place with pure broth and air when sterile

TABLE II.—Showing the Absorption of Dissolved Oxygen from Sterilised Tap Water containing a definite amount of Free Oxygen in solution, after sowing with 1 per cent. of a two days old Broth Cultivation, and incubating for a definite time  
Temperature of Incubation, 21–23° C

*Anaerobic Organisms.*

Organism	No 3	No 4	Blank expt
Original volume of oxygen dissolved	6 04	6 04	6 04
Residual oxygen	4 70	12	5 10
Oxygen absorbed	1 34	5 92	94
Duration of incubation	14 hours	14 hours	14 hours

*Aerobic Organisms*

Organism	No 1	No 1A	No 2	No 3	No 4
Original volume of oxygen dissolved	6 04	6 04	6 04	6 04	6 04
Residual oxygen	05	07	15	51	5 60
Oxygen absorbed	5 99	5 97	5 89	5 53	44
Duration of incubation	14 hours	14 hours	14 hours	14 hours	3 hours

Organism	No 4	No 4	No 5 *	No 6	No 6
Original volume of oxygen dissolved	6 04	6 04	6 04	6 04	6 04
Residual oxygen	20	07	20	4 00	1 32
Oxygen absorbed	5 84	5 97	5 84	2 04	4 72
Duration of incubation	21 hours	14 hours	14 hours	14 hours	42 hours

PREPARATION OF STERILE GELATINE TUBES AND METHOD OF PLATE CULTURE USED.

As the method of preparing sterile gelatine tubes used by the authors is somewhat simpler and shorter than that usually adopted, the details are here appended

(1) The test tubes, 5 or 6 inches  $\times \frac{3}{4}$ , are first washed and set up on end to drain and then heated to 150° for an hour in the steriliser.

(2) Pure cotton-wool is placed in a *steam* steriliser and subjected to a current of

\* Four days old broth (slow-growing organism)

wet steam for two hours, and afterwards dried in the *hot air* steriliser by heating to  $150^{\circ}\text{C}$  for half an hour. This method of sterilising the wool is to be preferred to the usual one of heating in the hot air steriliser for several hours on several successive days, not only on account of the saving in time, but also because it gives a white wool without brittle and partly charred threads. The treatment is quite effective, steam at  $100^{\circ}\text{C}$  being a better germicide than hot dry air at the same temperature. By this method sterile plugged tubes can be prepared in one day instead of requiring several days.

(3) The sterile tubes are now plugged in the usual way, using clean fingers to manipulate the wool. When about half a gross of tubes are thus plugged they are again placed in the hot air steriliser and raised to  $150^{\circ}\text{C}$  for an hour.

*Preparation of Sterile Nutrient Gelatine*—One pound of lean beef free from fat is finely minced and placed in a large beaker with clock glass cover. A litre of tap water is poured over the mass and the whole placed in the steam steriliser for one and a half hour, stirring the mass to mix thoroughly after the first half hour. After one and a half hour's steaming the liquid is filtered into another large beaker containing—

100 grms. of gelatine

10 grms. of peptone.

5 grms. of salt

The hot filtrate quickly dissolves the gelatine, and the mass should be stirred until the sheets are broken up and dissolved. The mixture is now placed in the steam steriliser for half an hour, neutralised with potassium carbonate, and replaced in the steriliser for another hour. The turbid fluid is now filtered into a large flask without any sterilising precautions whatever, and distributed in the usual manner to the sterile plugged tubes. The half gross of plugged and filled tubes are now placed together in a potato steamer and steamed for fifteen minutes. Steaming is repeated on the second and third day for ten minutes each day.

The authors find this treatment quite effective, the tubes obtained never show the least growth on keeping. Out of many hundreds of tubes only two have shown any growth, and both, on examination, proved to be cracked tubes, and probably the cold water bath, in which the tubes are placed to set, introduced organisms through the crack.

Before opening the tubes the tuft of wool was uniformly singed to burn up the dust and germs which might have fallen on the outside.

*Preparation of Sterile Peptone Broth.*—For this the 100 grms. of gelatine is omitted, otherwise exactly the same method is used.

*Preparation of Sterile Agar Agar.*—For the 100 grms. of gelatine 20 grms of agar agar are employed.

*Plate Cultivations*—Shallow covered glass dishes about a decimetre in diameter

and 15 millims. deep (known as Petri's dishes) were uniformly used. These are much more simple to work with and give less contamination from the air than the original glass plate and bell-jar method. Three plates were poured for each cultivation, containing successively smaller amounts of material, so as to ensure a good plate.

In isolating organisms from sewage a second series of plates was always made to ensure perfect purity, the first apparently pure colony often covering a less conspicuous one.

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FOR THE YEAR 1891

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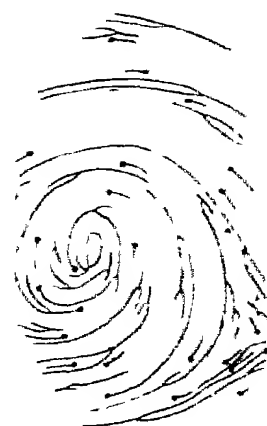


West, Newman, Photo lith

Plate 1. Eight cases in which the impression of a finger or thumb has been repeated after an interval of many years

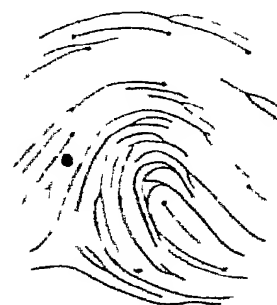






1 A E H F r

5 H F r



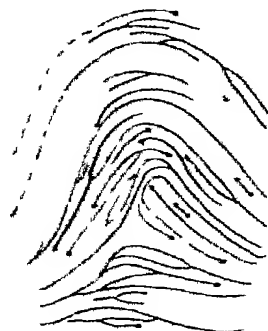
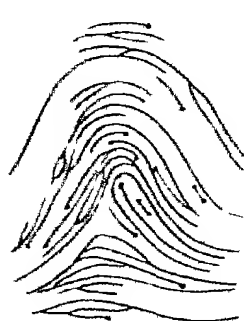
2 A E H F 3r

6 R F H 2r



3 N H T 1r

7 W J H thumb, r



4 N H T 2r

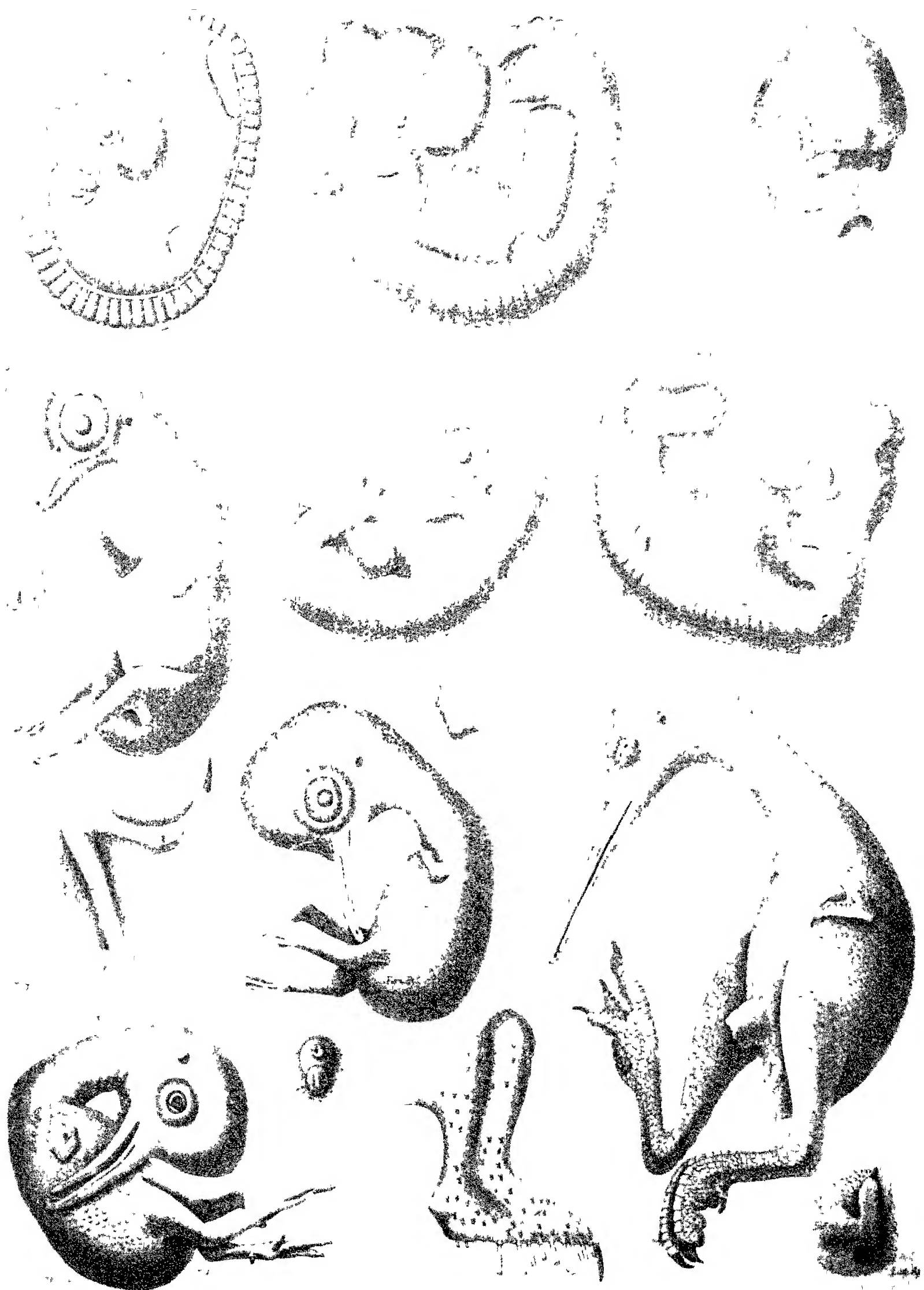
8 W J H 3r

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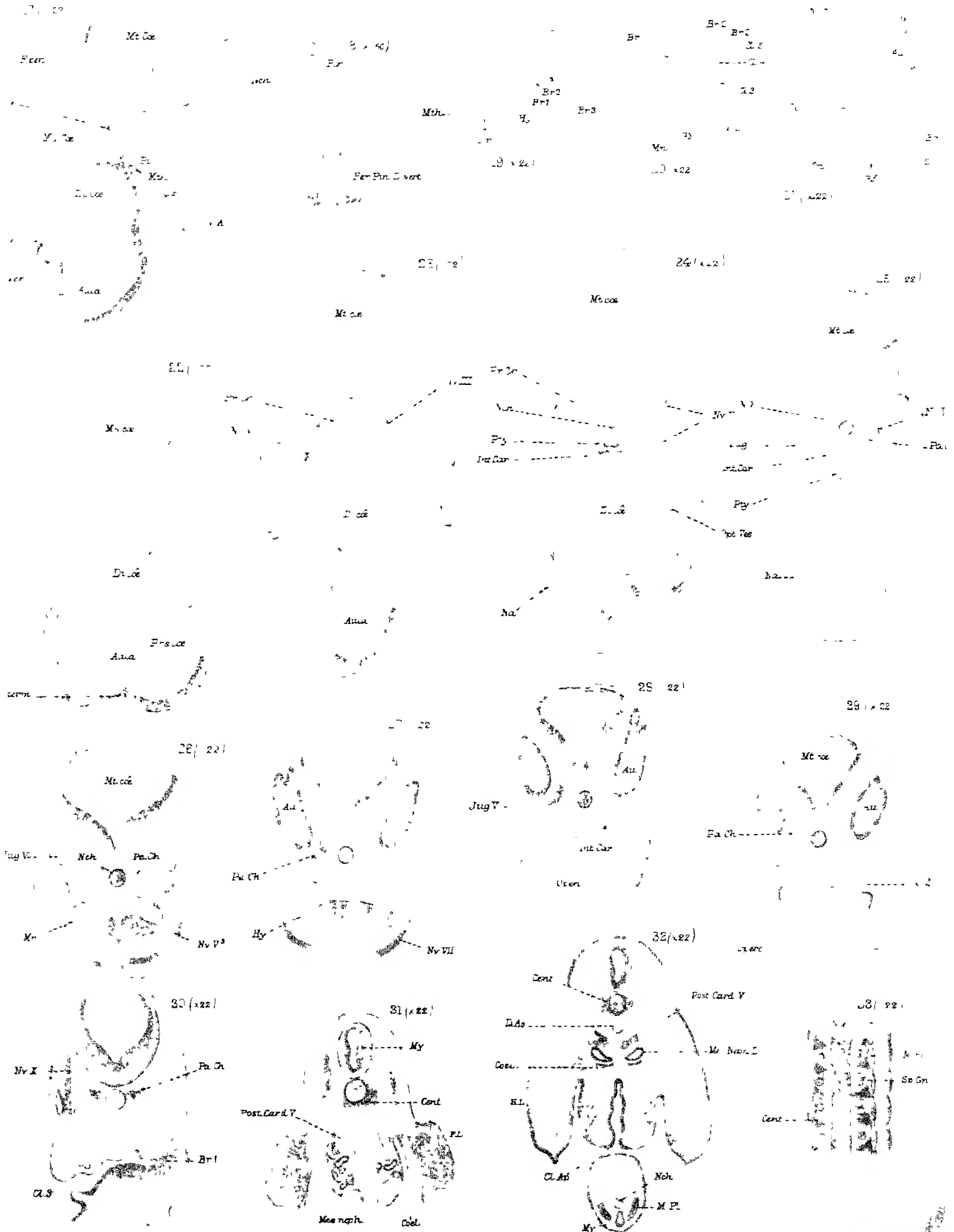
Plate II Skeleton maps of the impressions in Plate I, showing the places where ridges begin, through bifurcation or independently











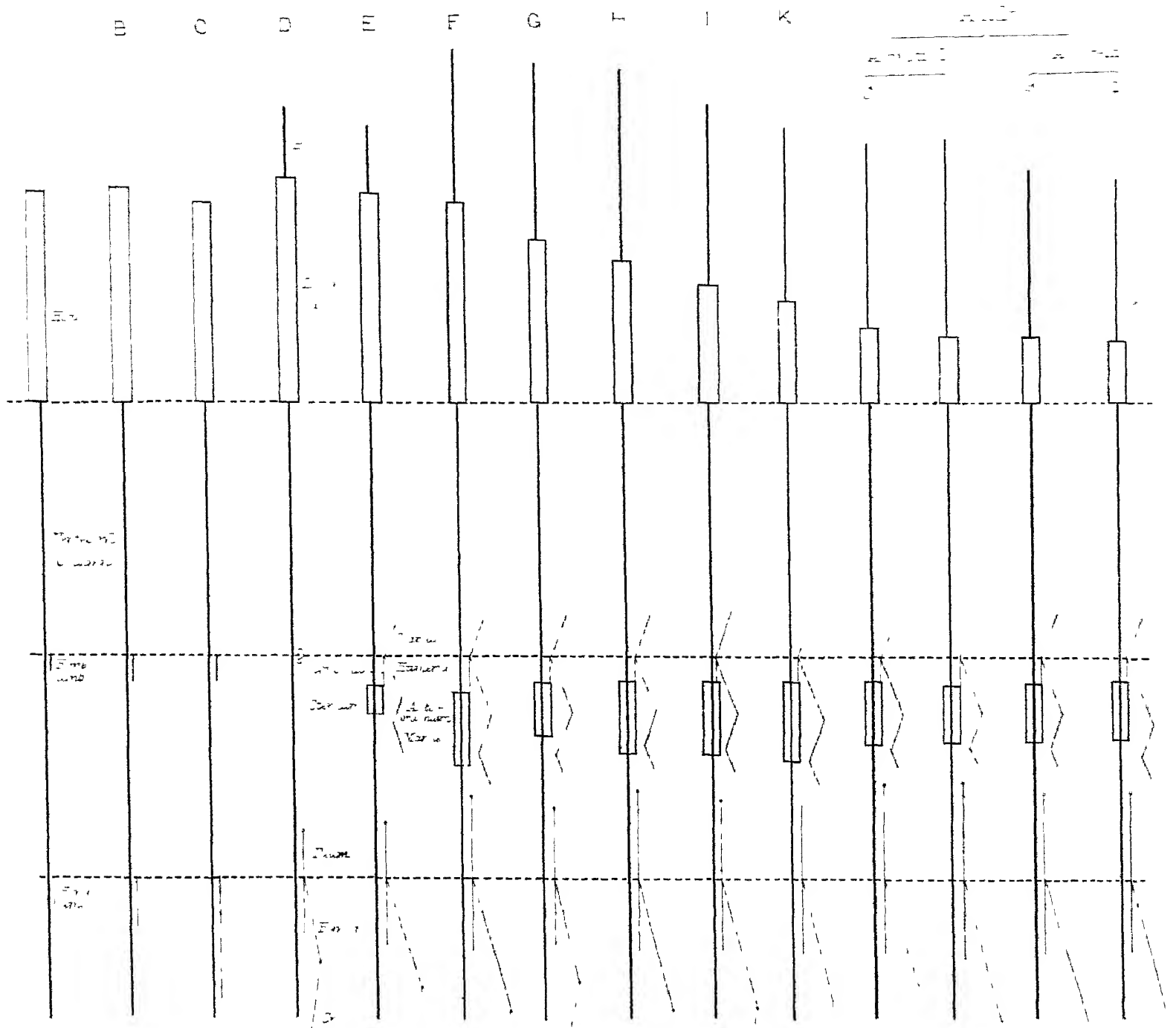
TJ Pad nat del  
MCP Parker chr lith

APTERYX Sections of Stages A and B



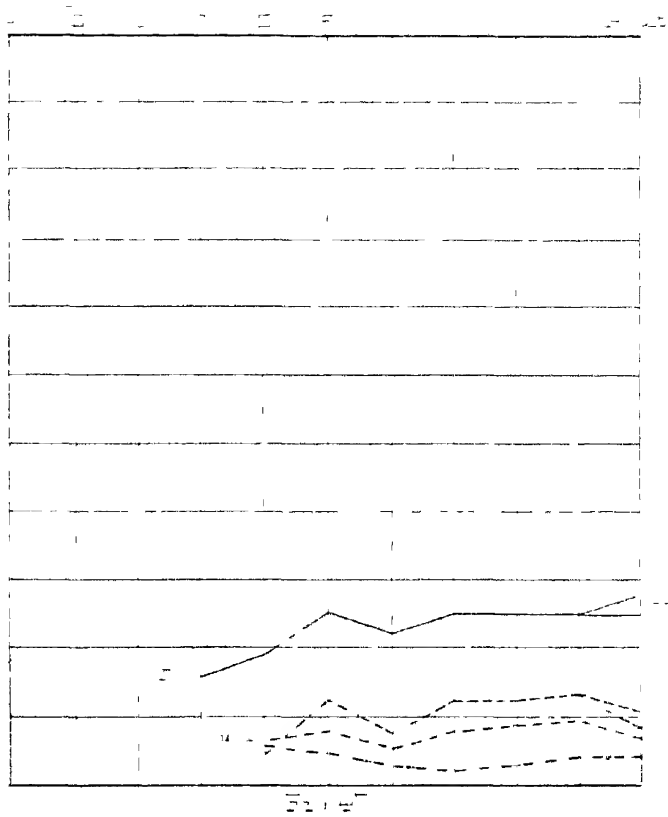
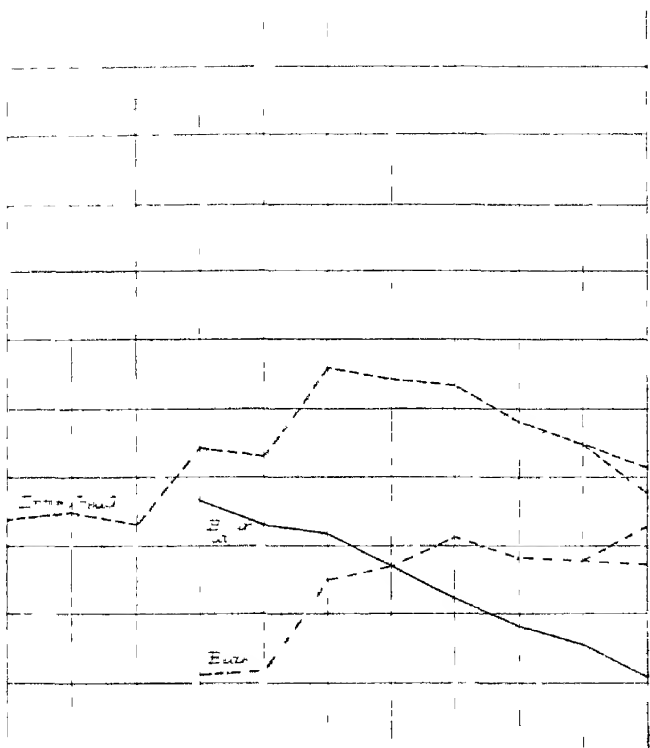












Length of Ventral Column = 1.0

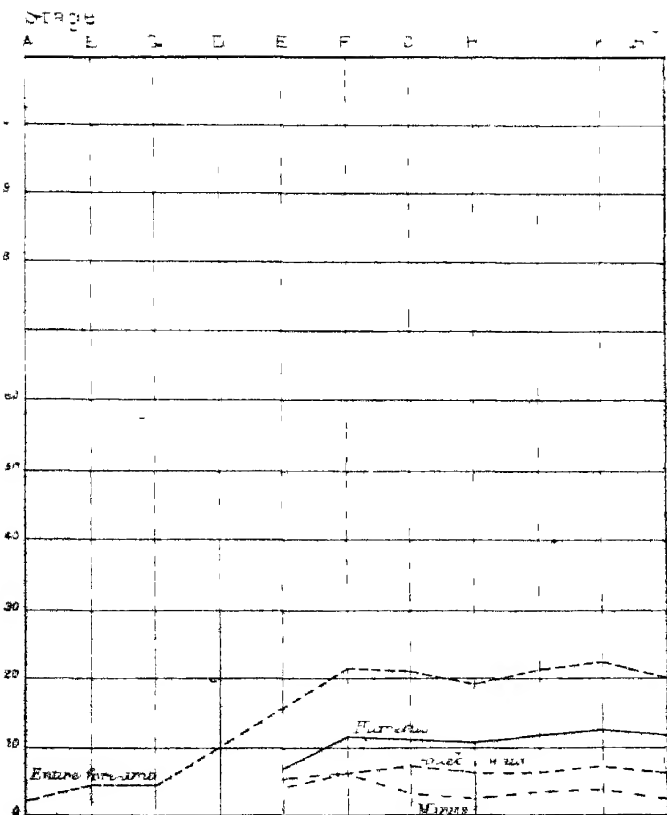


Fig 48

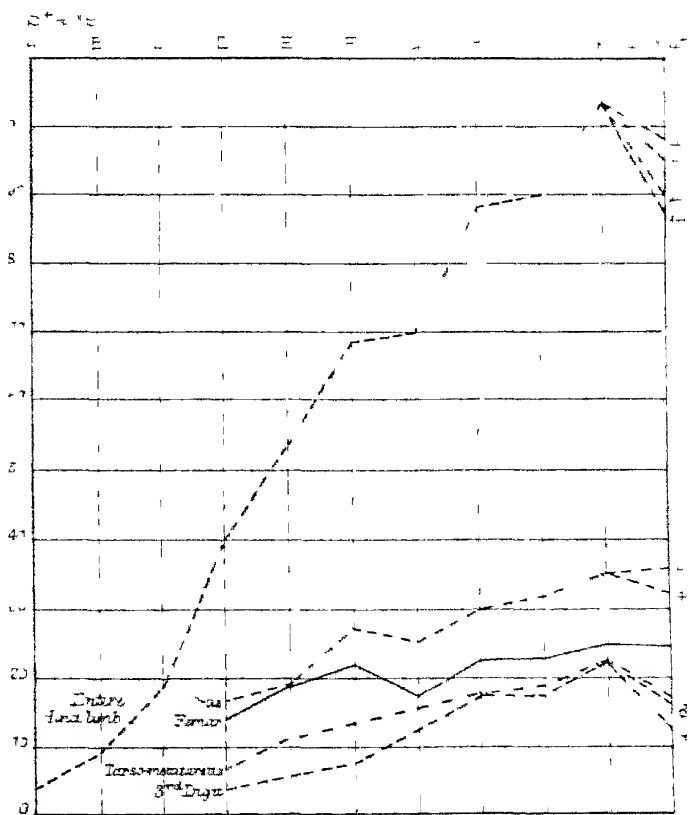
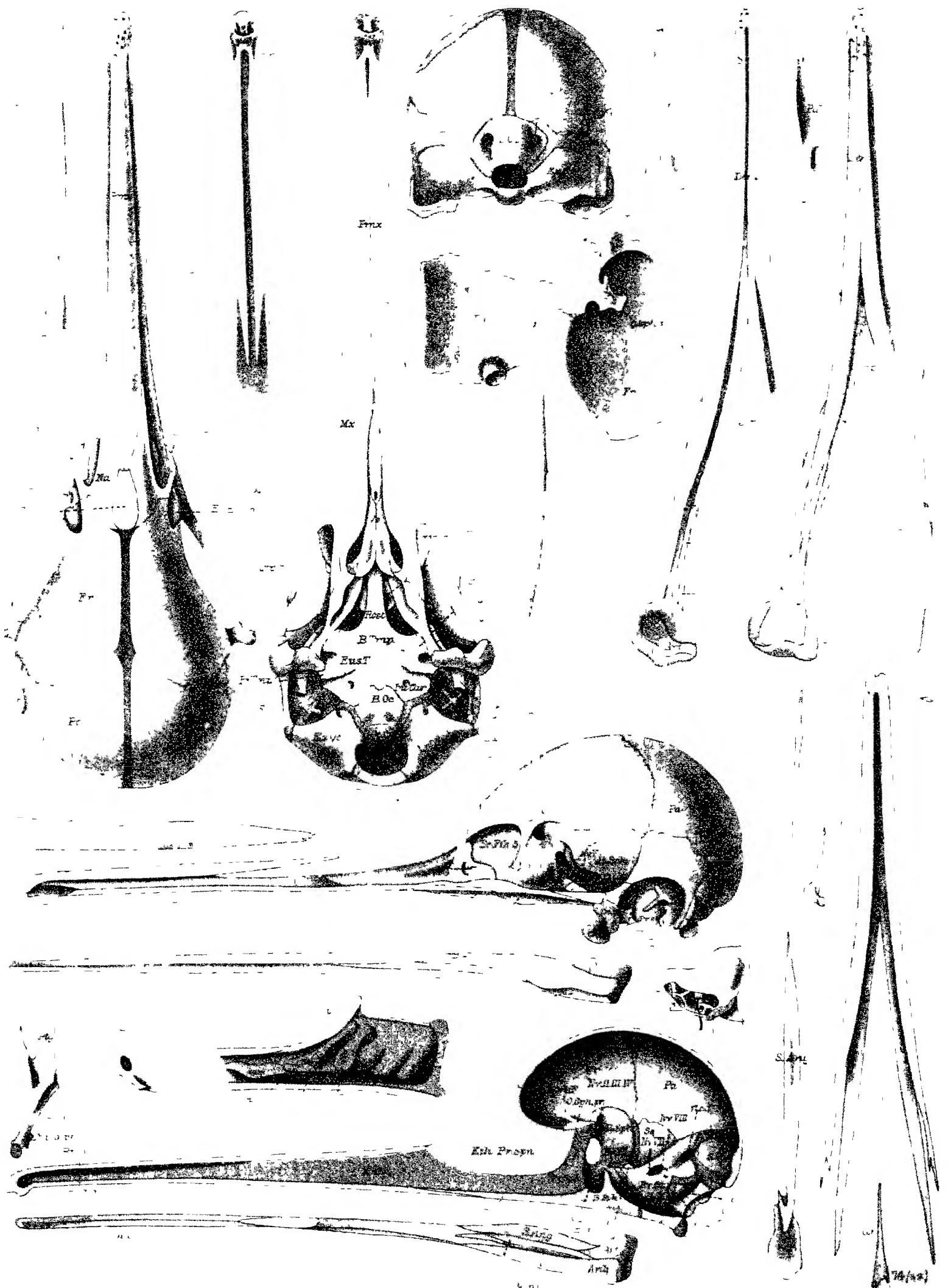


Fig 49

W.P. ad nat. del<sup>+</sup>  
M.P. Parker lith

West Newman engr.



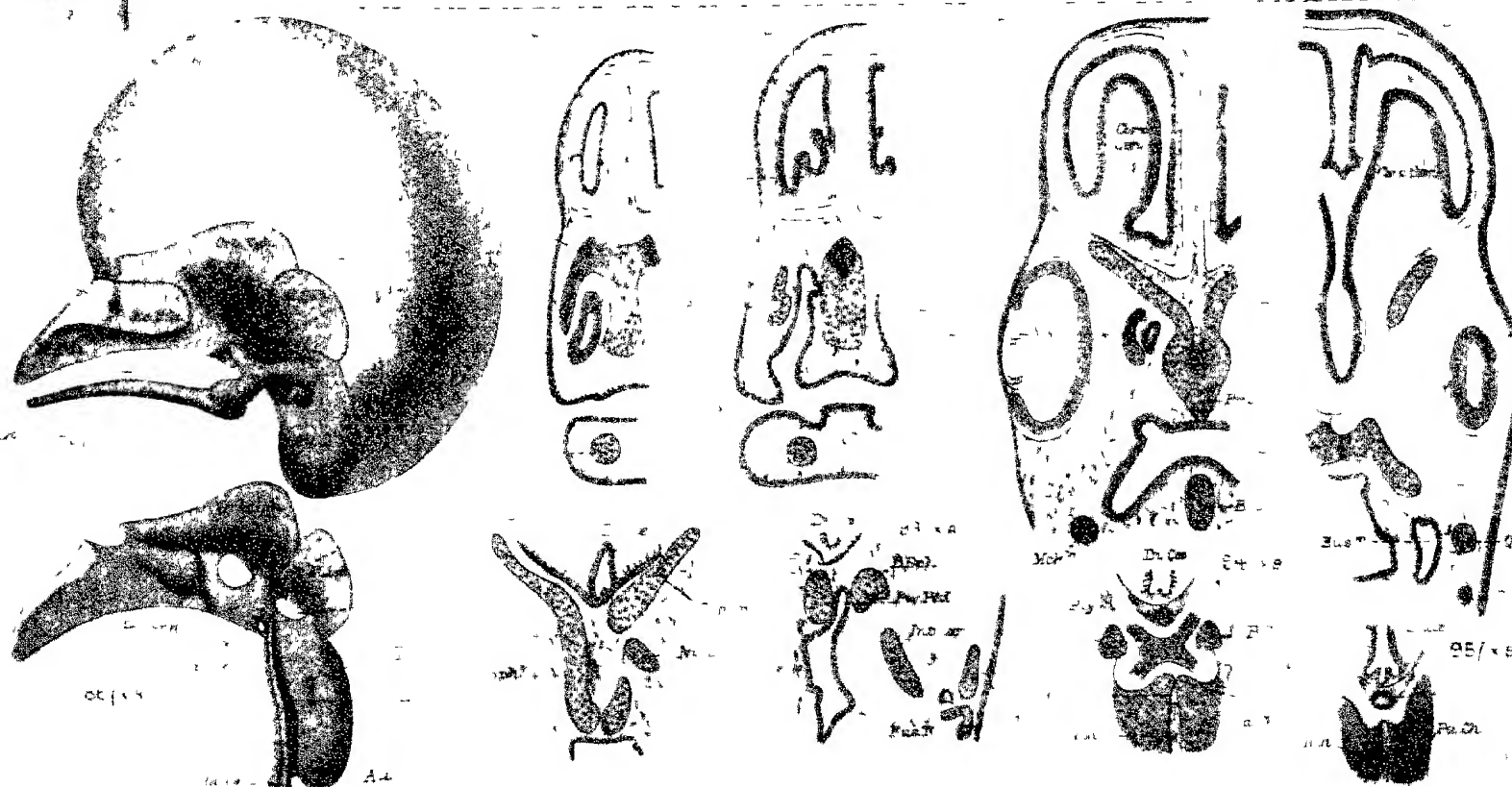
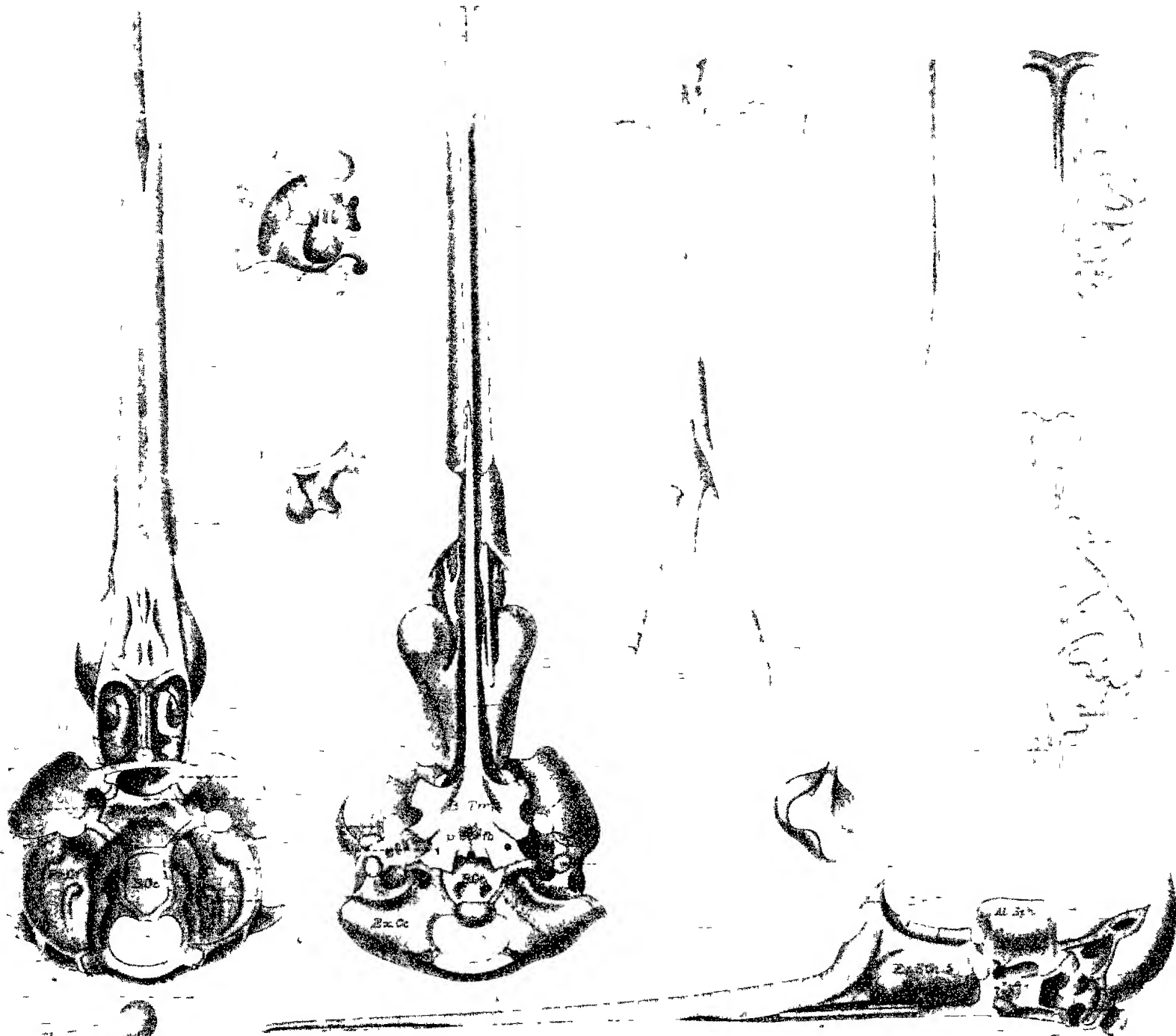


TJ Pad nat del<sup>s</sup>  
MP Parker chr htl.

APTERIX Skull of ripe embryo (Stage K)

West. Newman 1891











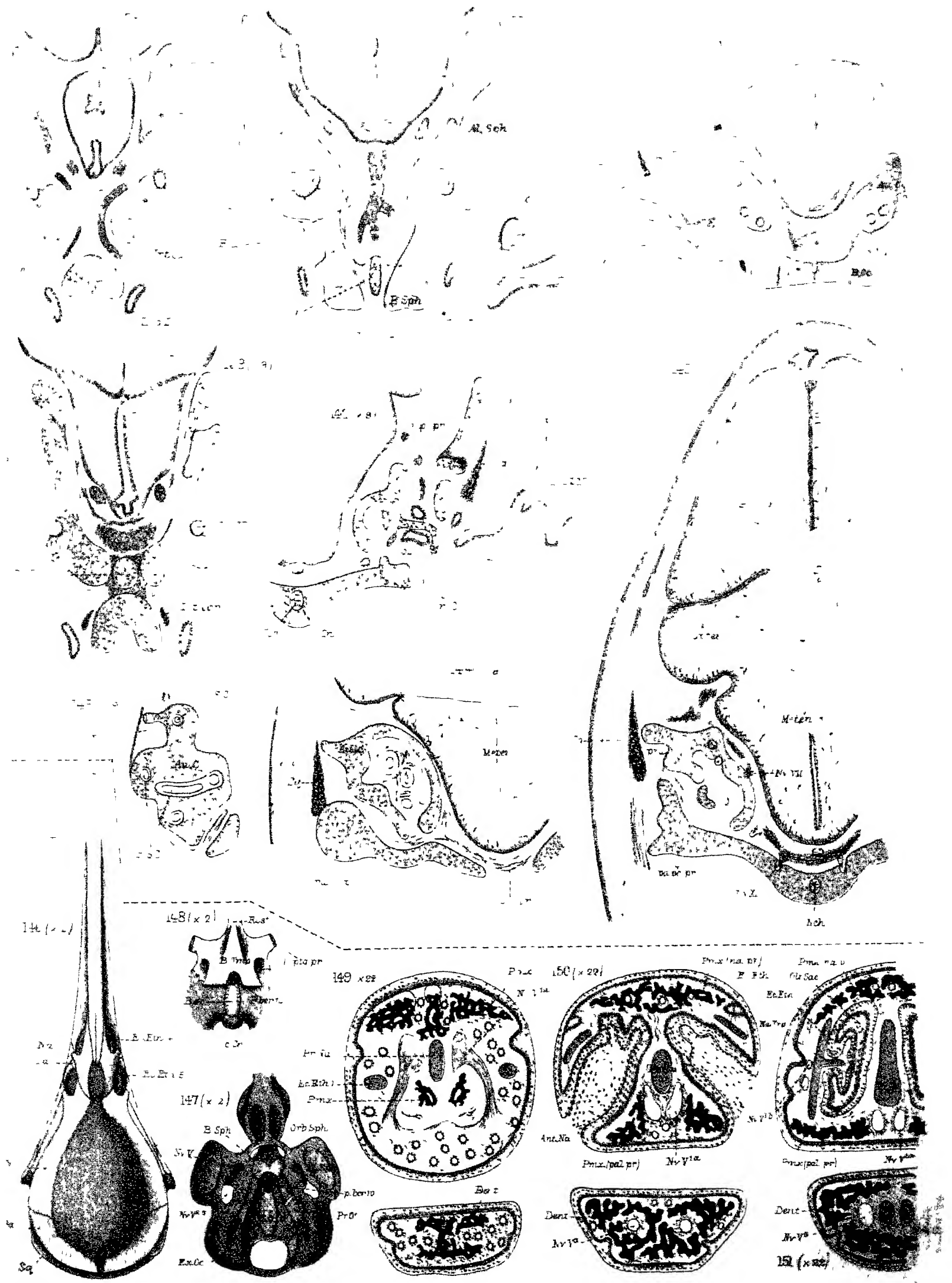
TJF ed natchel<sup>†</sup>  
MP Parker chr lth

**West, Kenneth J.**





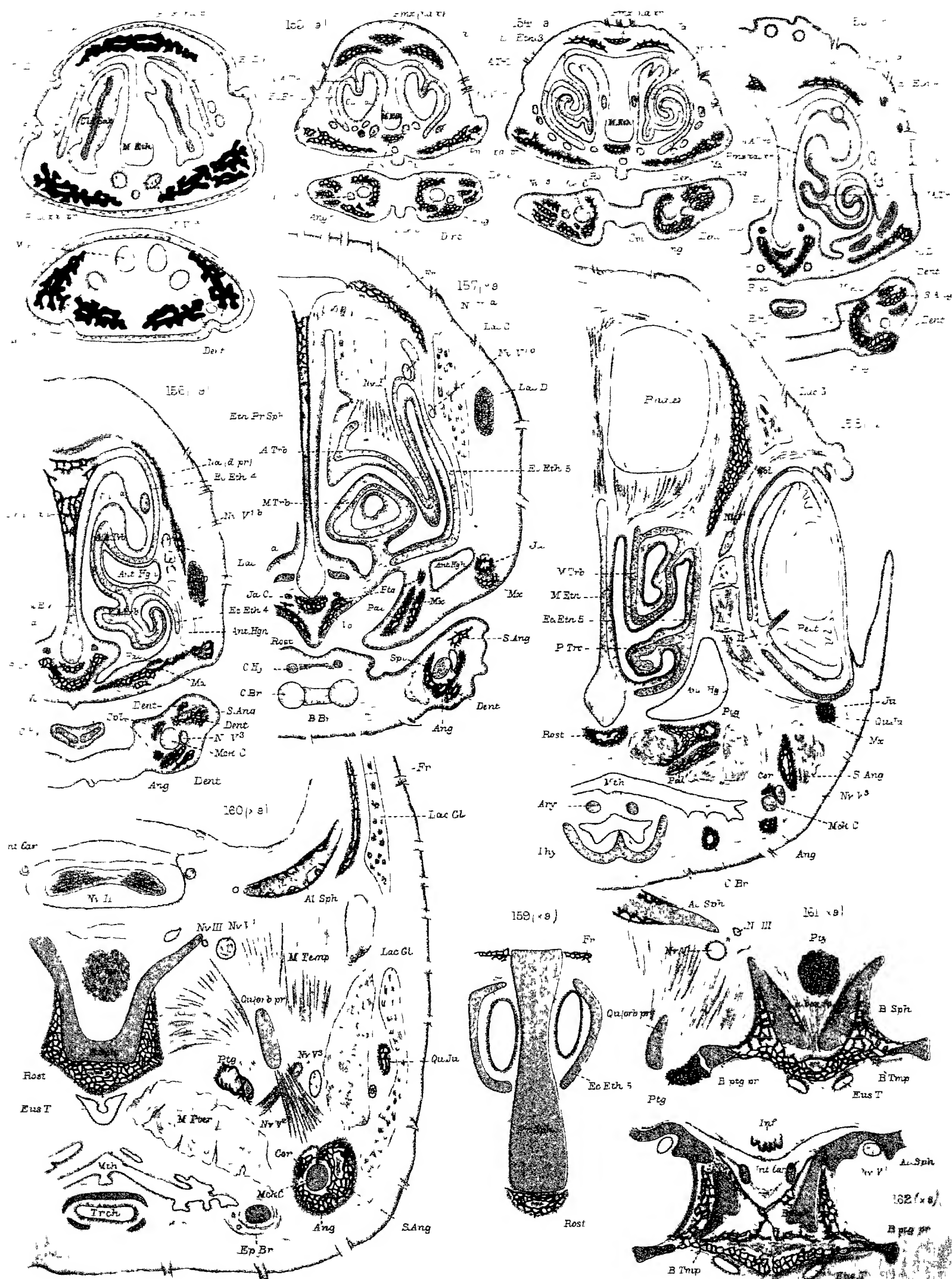




APTERYX Skull. Stages G and H

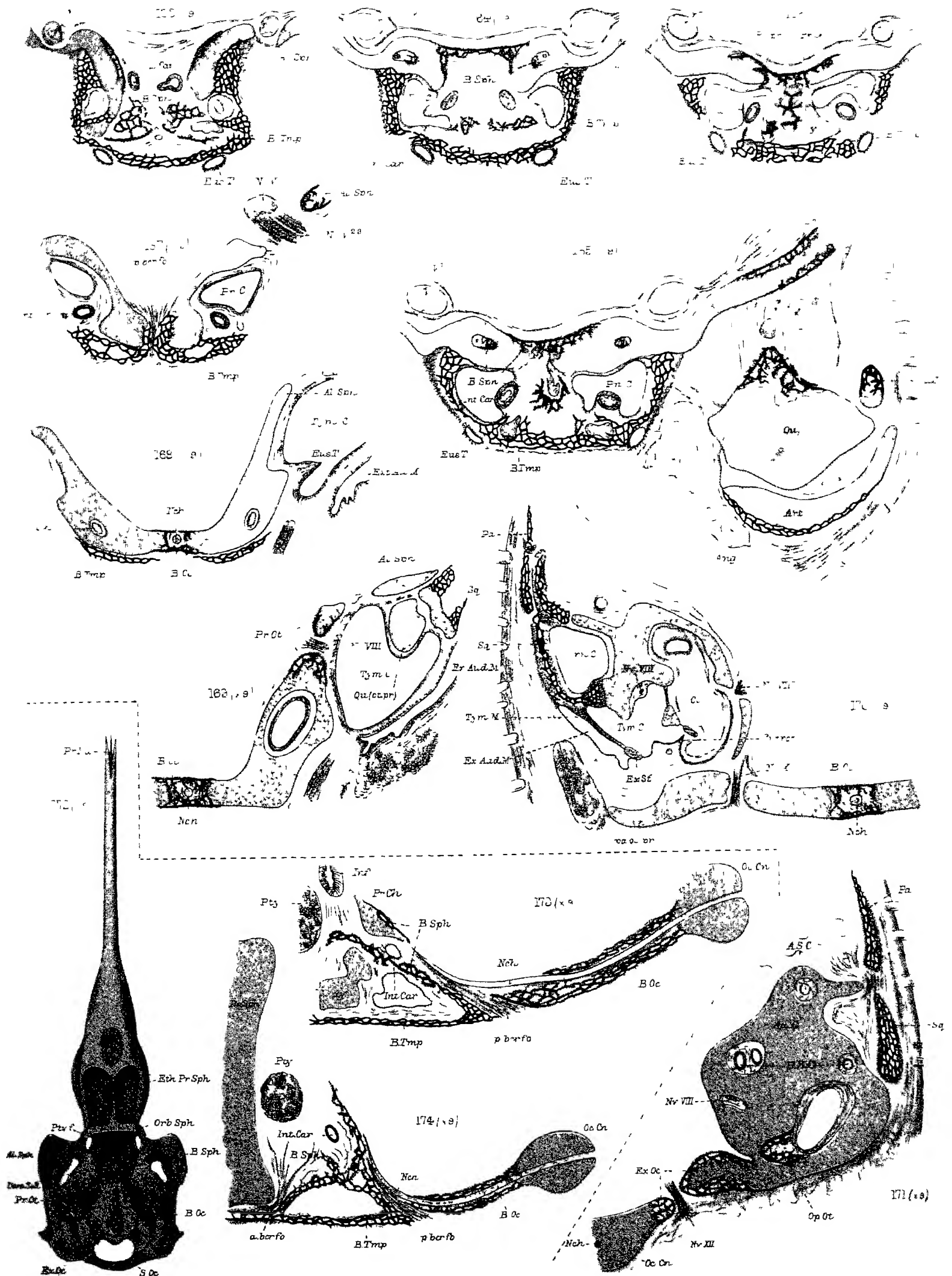
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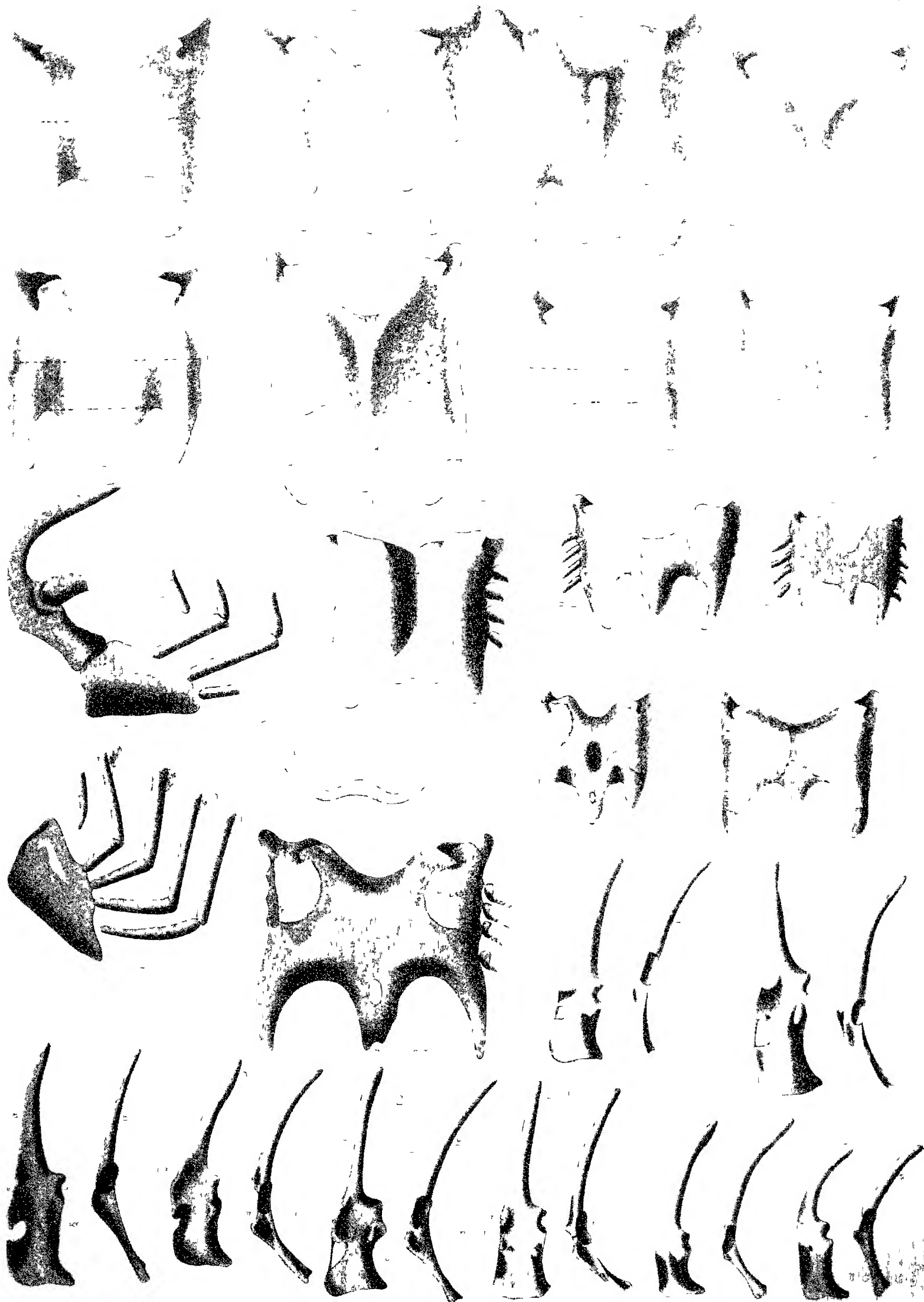






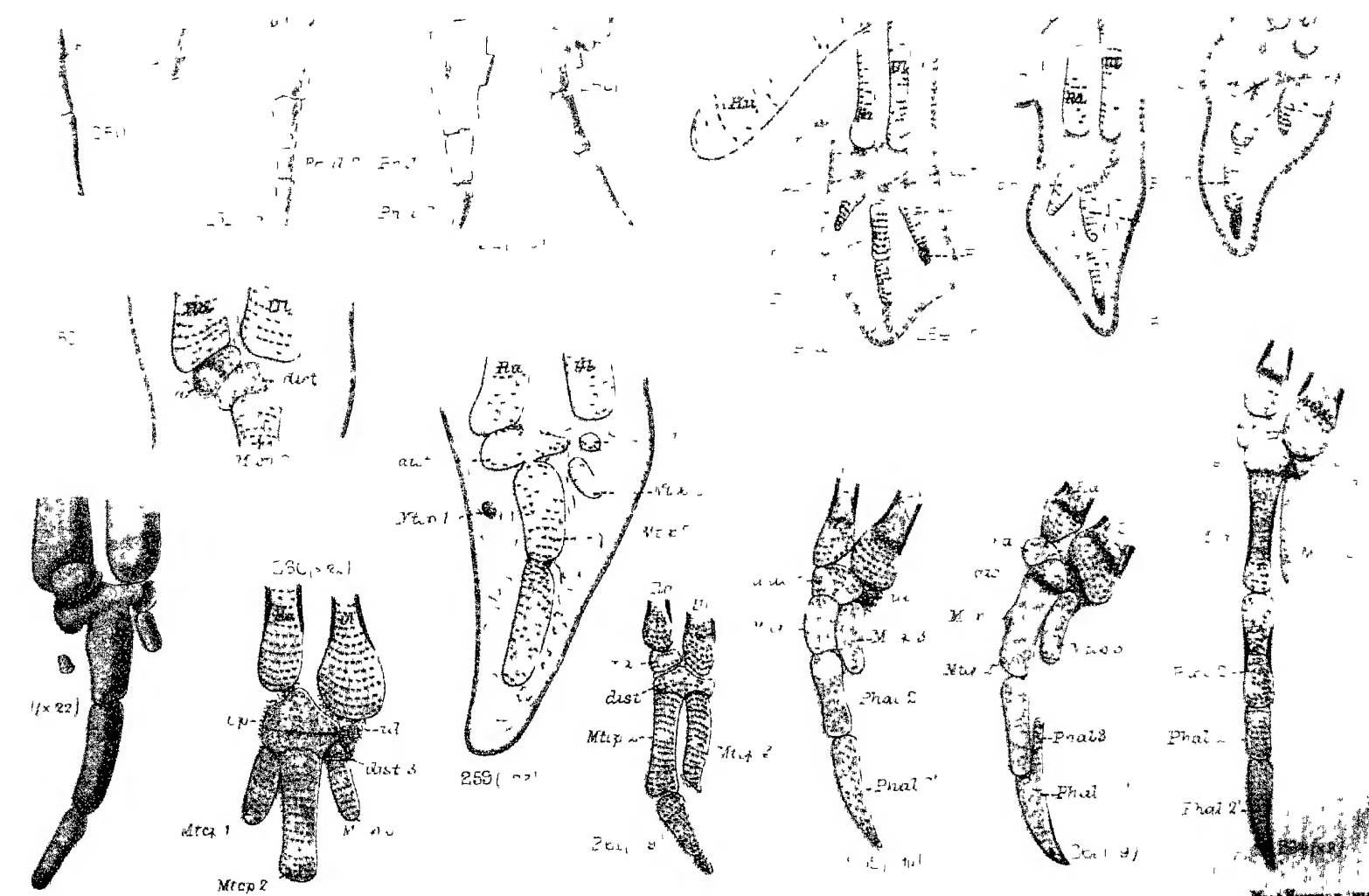
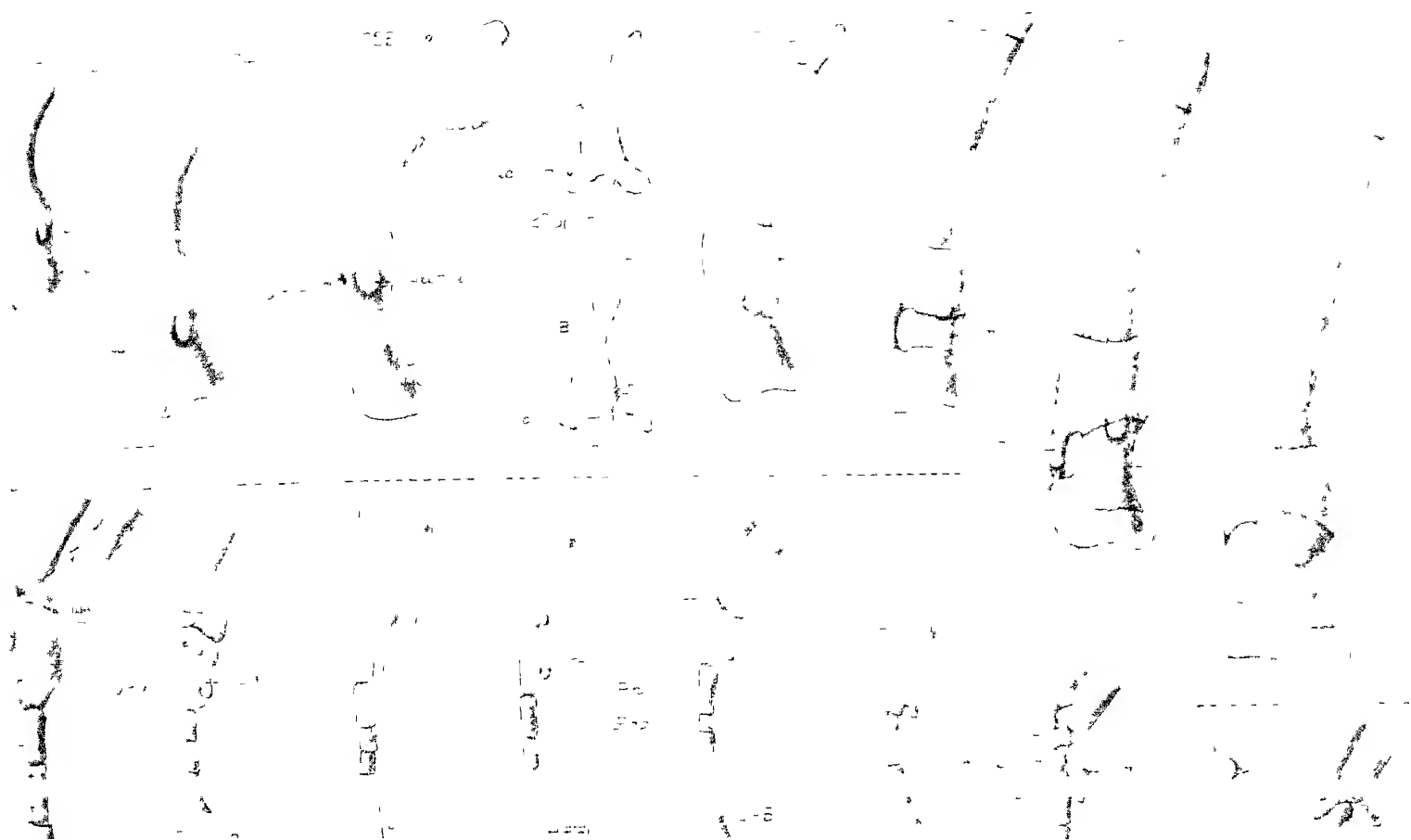








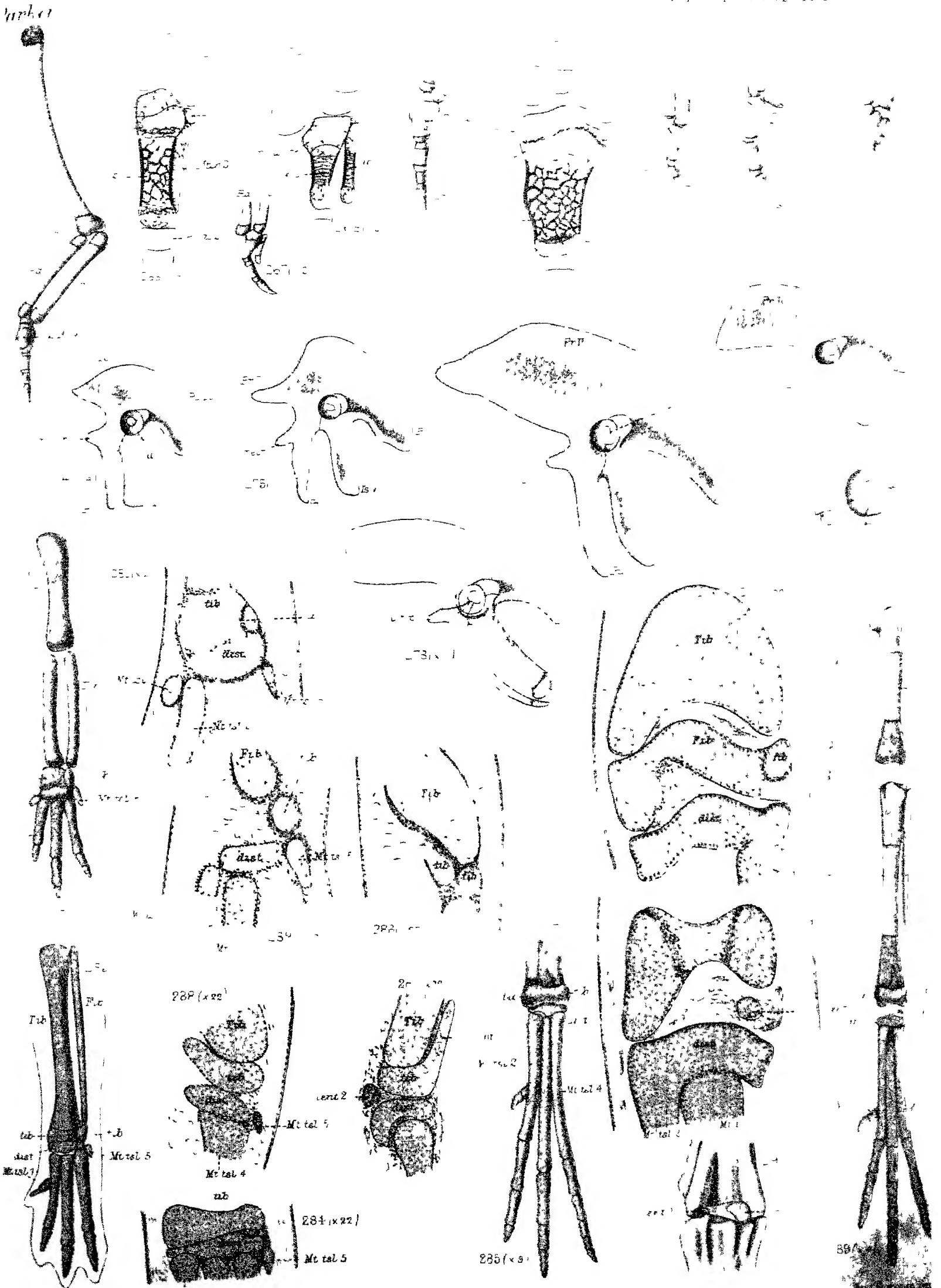




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MPParker chr hch

West Herring 1891

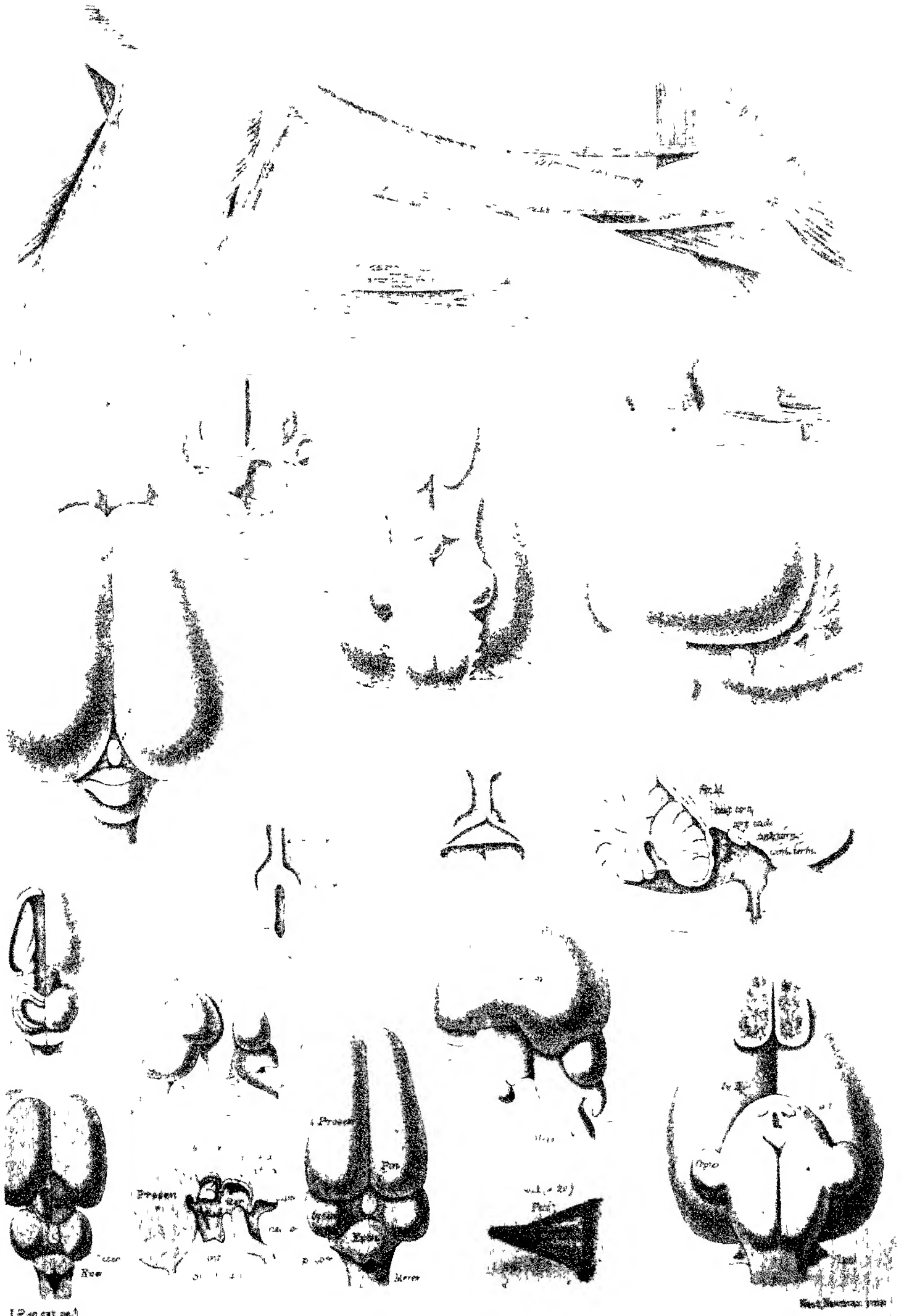




J.J.P. adnat del.  
M.P. Parker chir. lith.

APTERYX Fore-limb, Pelvic Girdle and Hind-limb





1. Pterostigma  
2. Pterostigma

APTERYX Muscles of Wing Branches and Veins



Fig 1

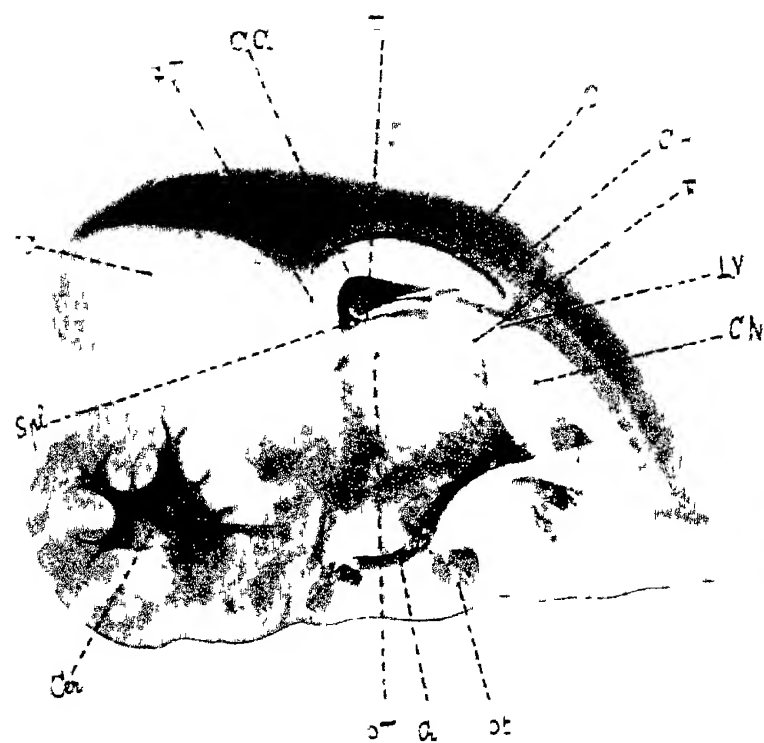


Fig 2



Fig 3

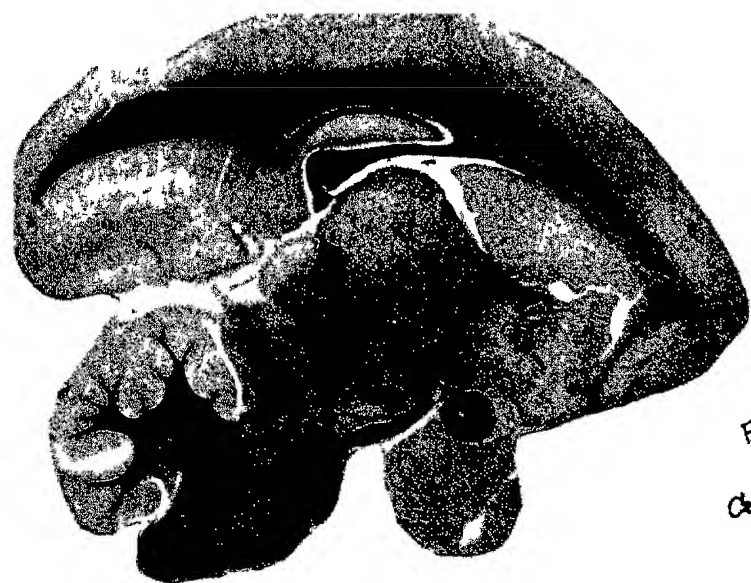
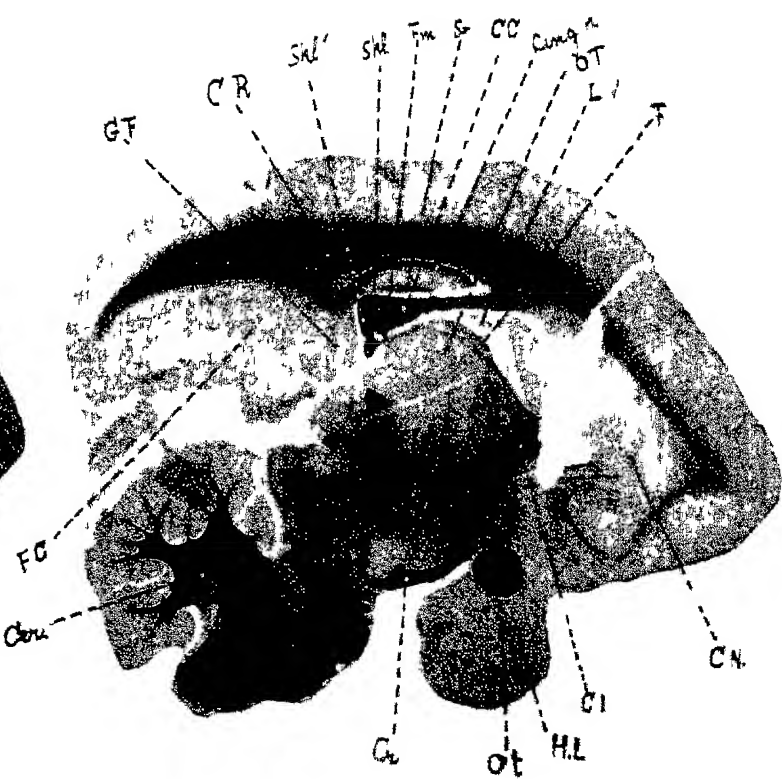


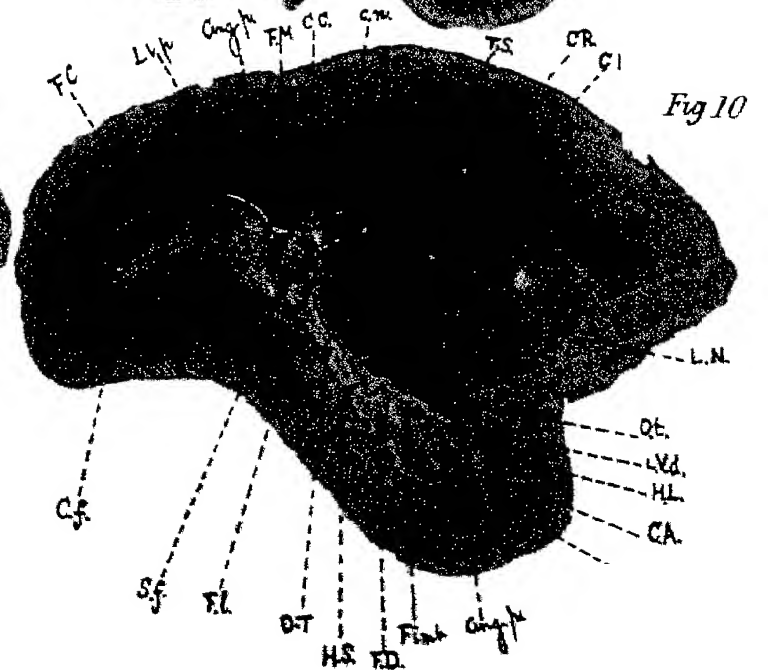
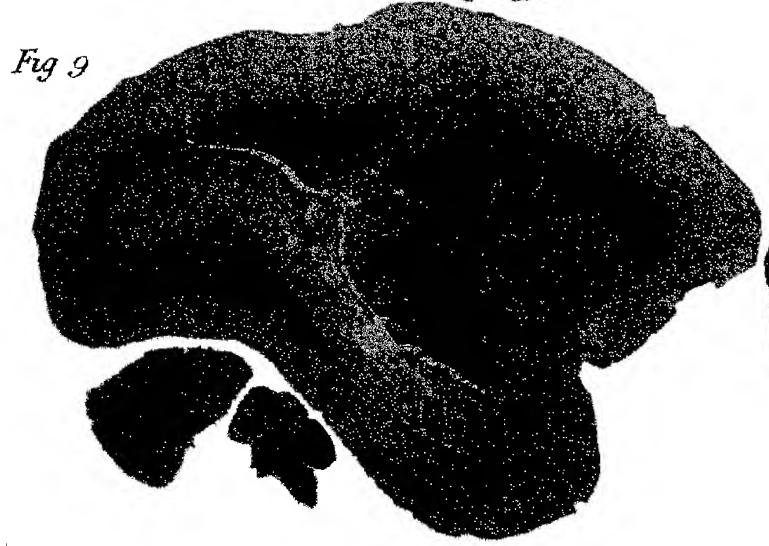
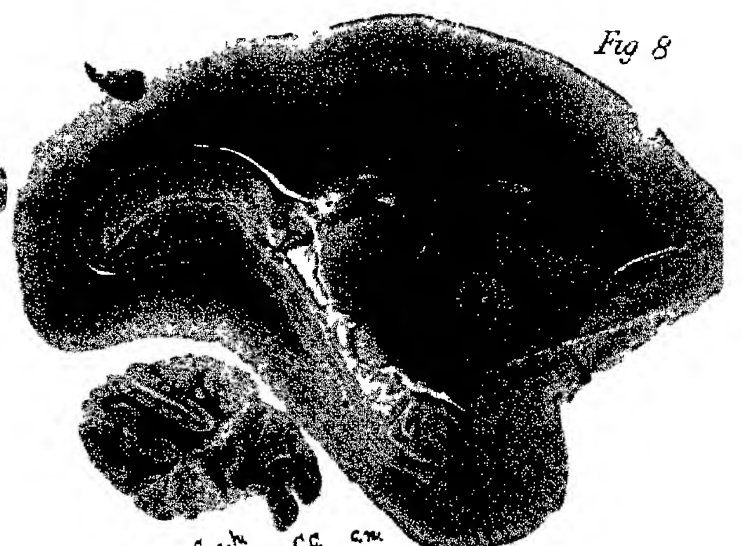
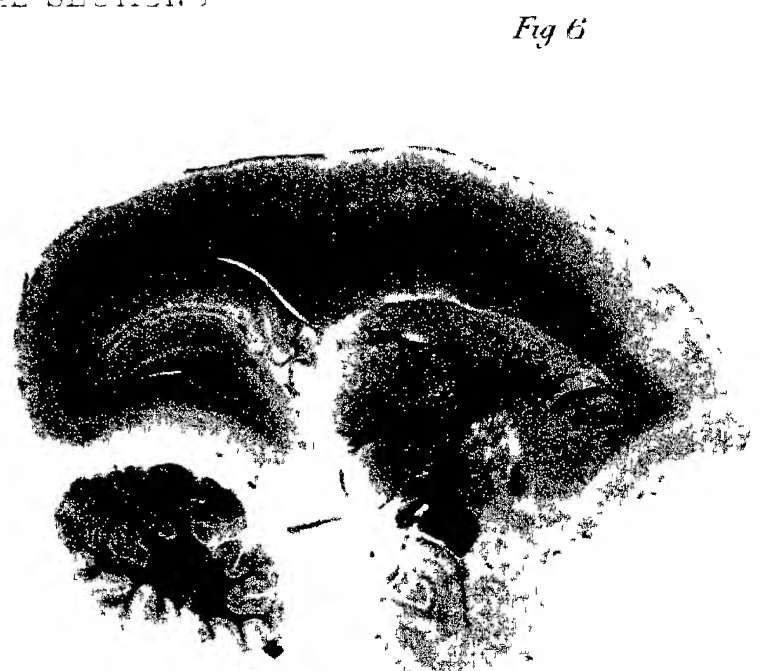
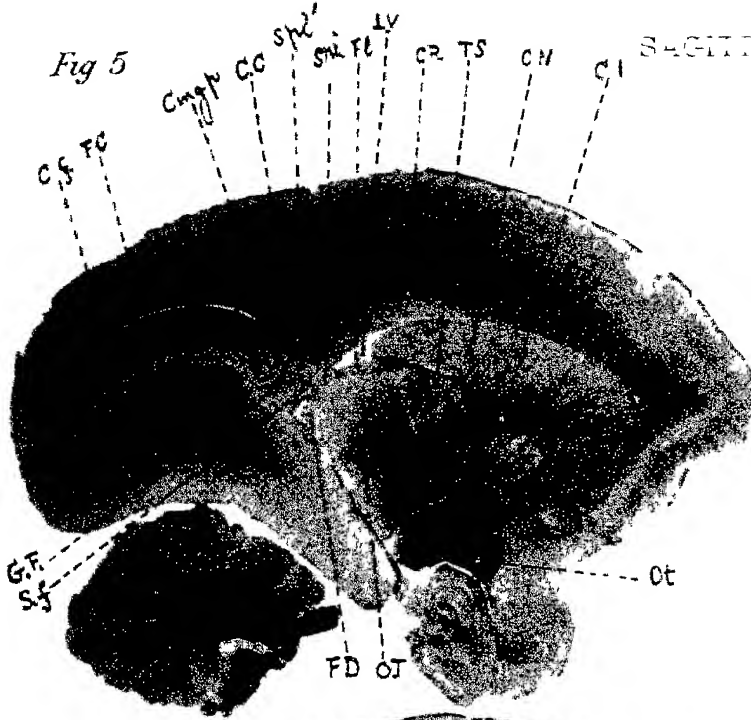
Fig 4





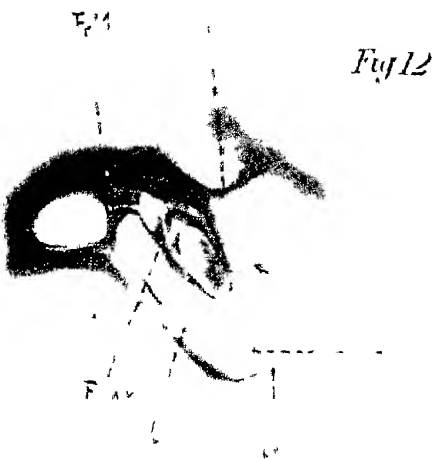
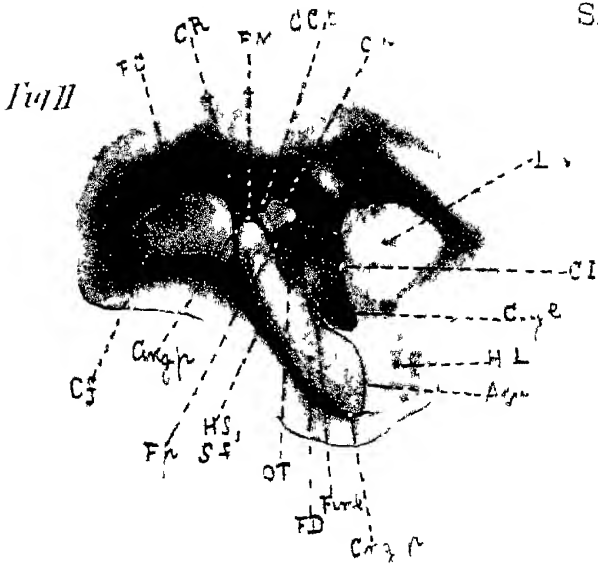


SAGITTAL SECTIONS



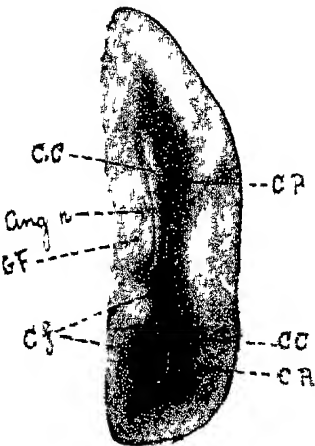


SAGITTAL SECTIONS

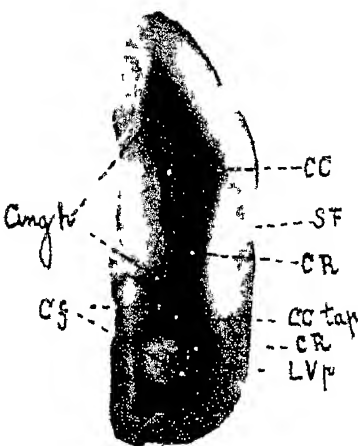


HORIZONTAL SECTIONS

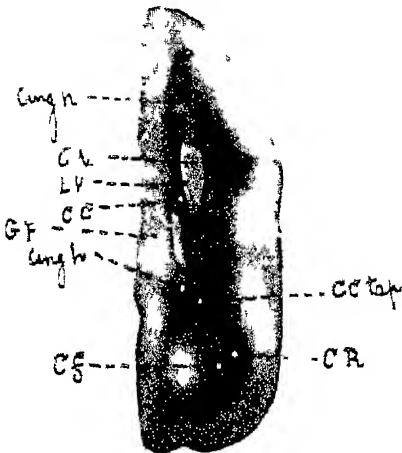
*Fig 15*



*Fig 14*



*Fig 15*



*Fig 16*

*Fig 17*

*Fig 18*

*Fig 19*

*Fig 20*

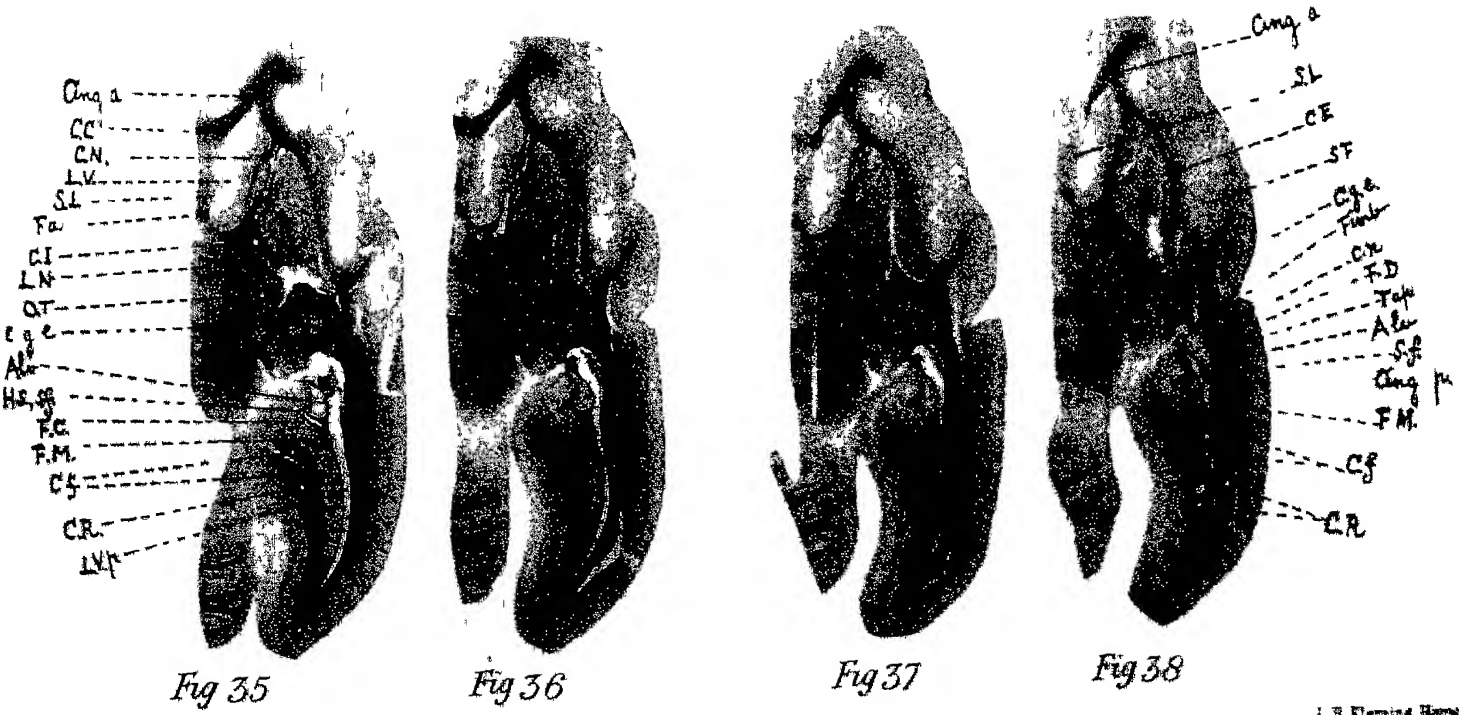
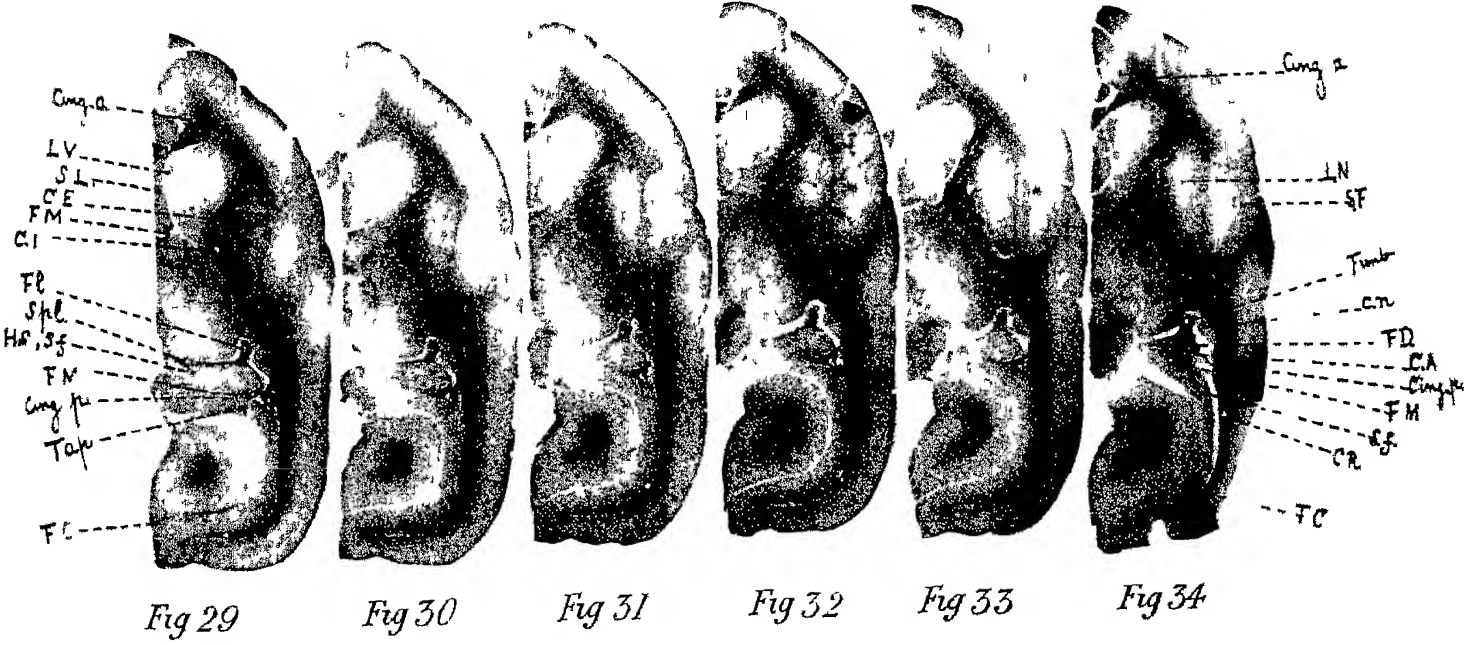
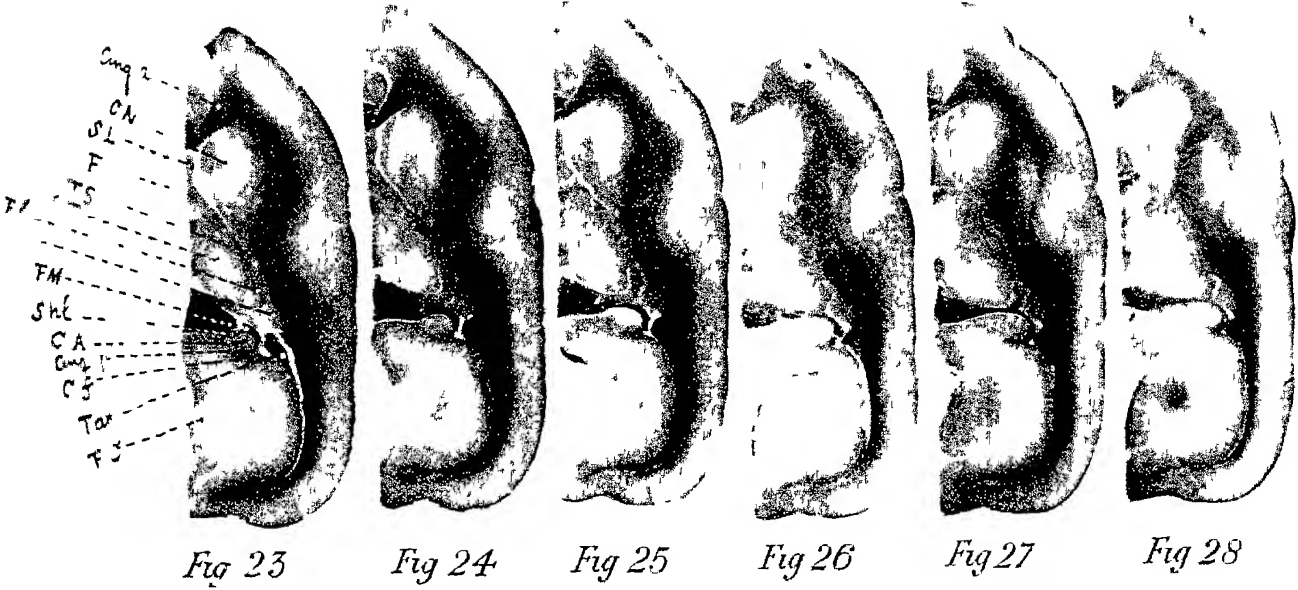
*Fig 21*

*Fig 22*



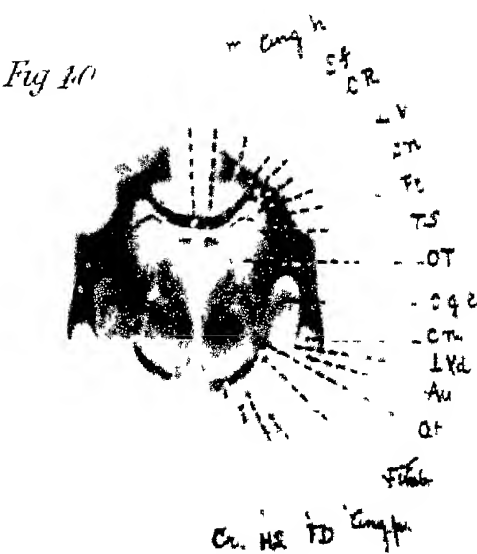
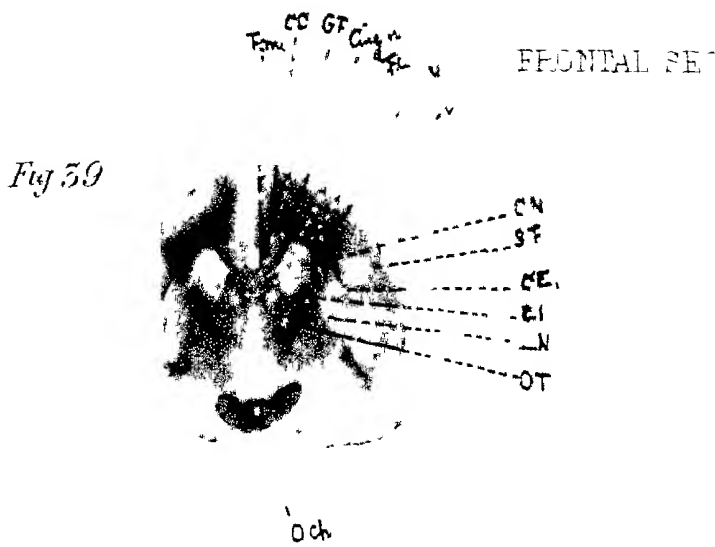


HORIZONTAL SECTIONS









FRONTO-OBSLQUE SECTIONS

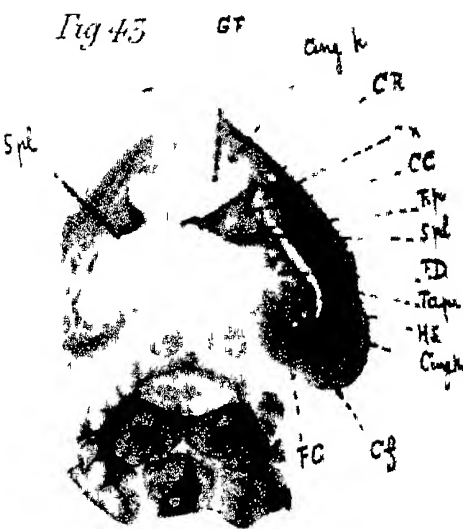
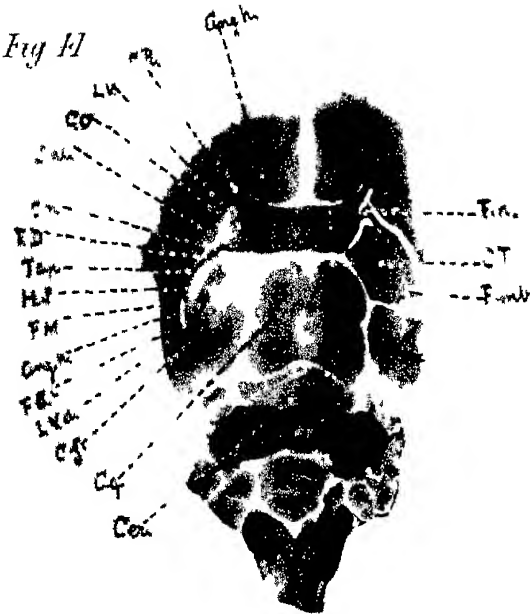


Fig 44

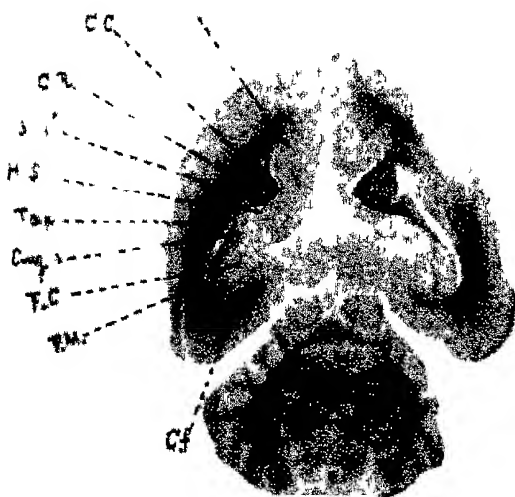


Fig 45

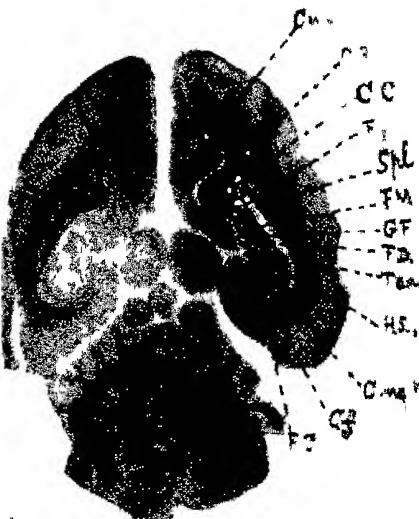




Fig 4

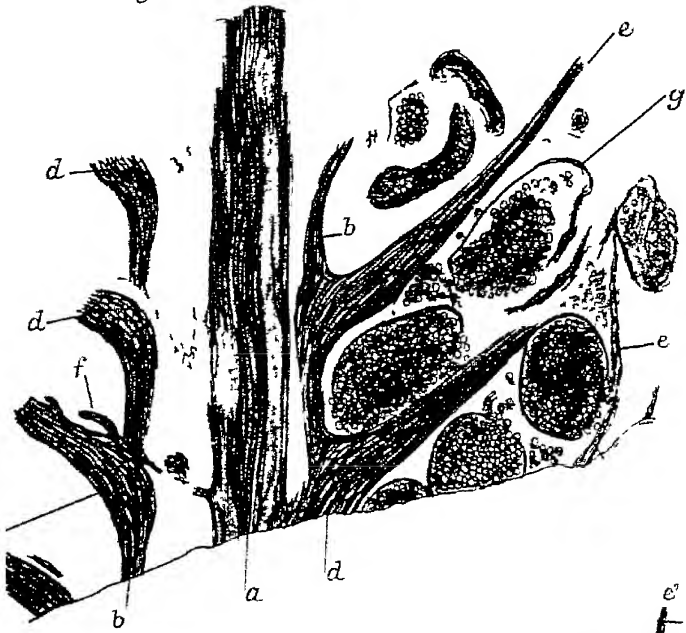


Fig 1

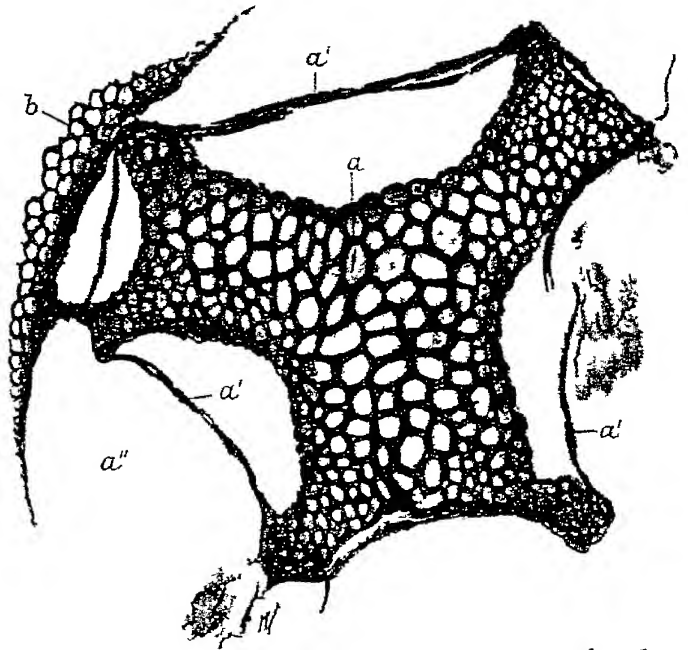


Fig 8

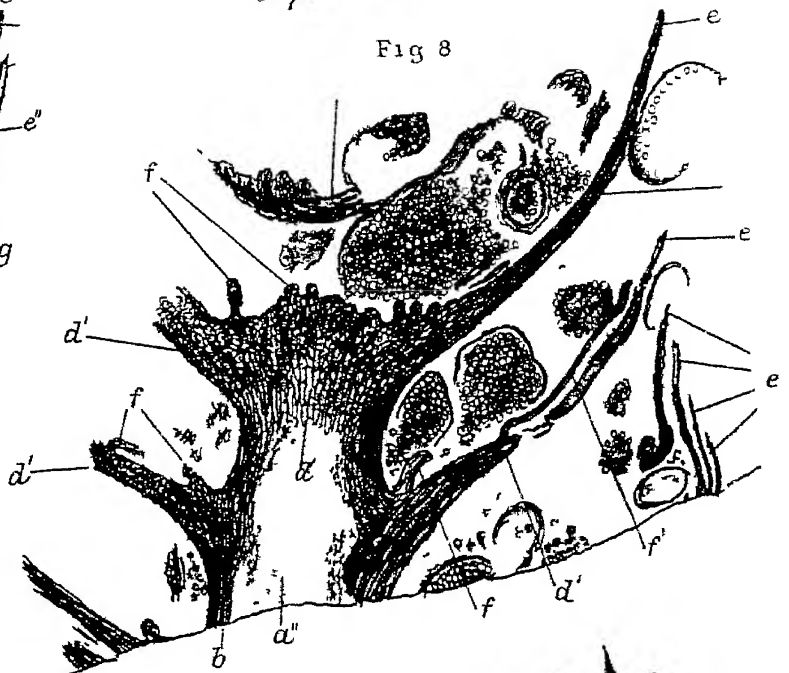


Fig 10

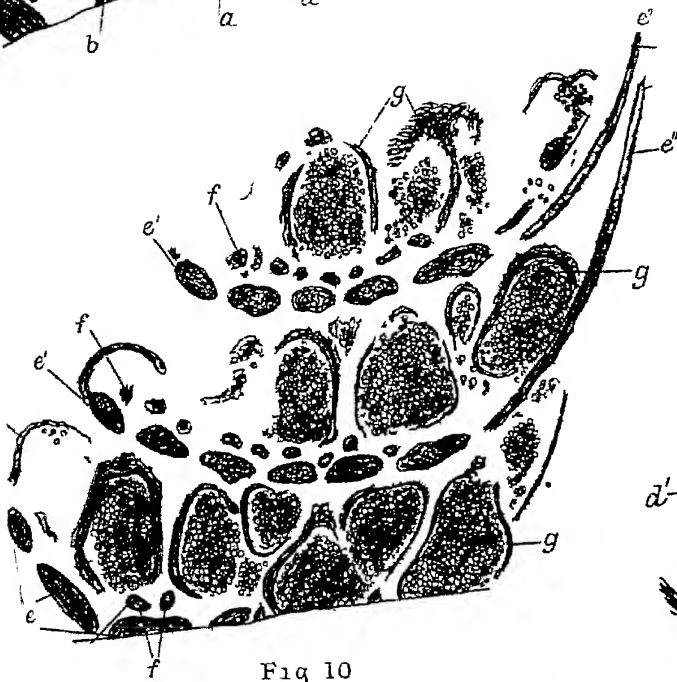


Fig 17



Fig 18



Fig 20

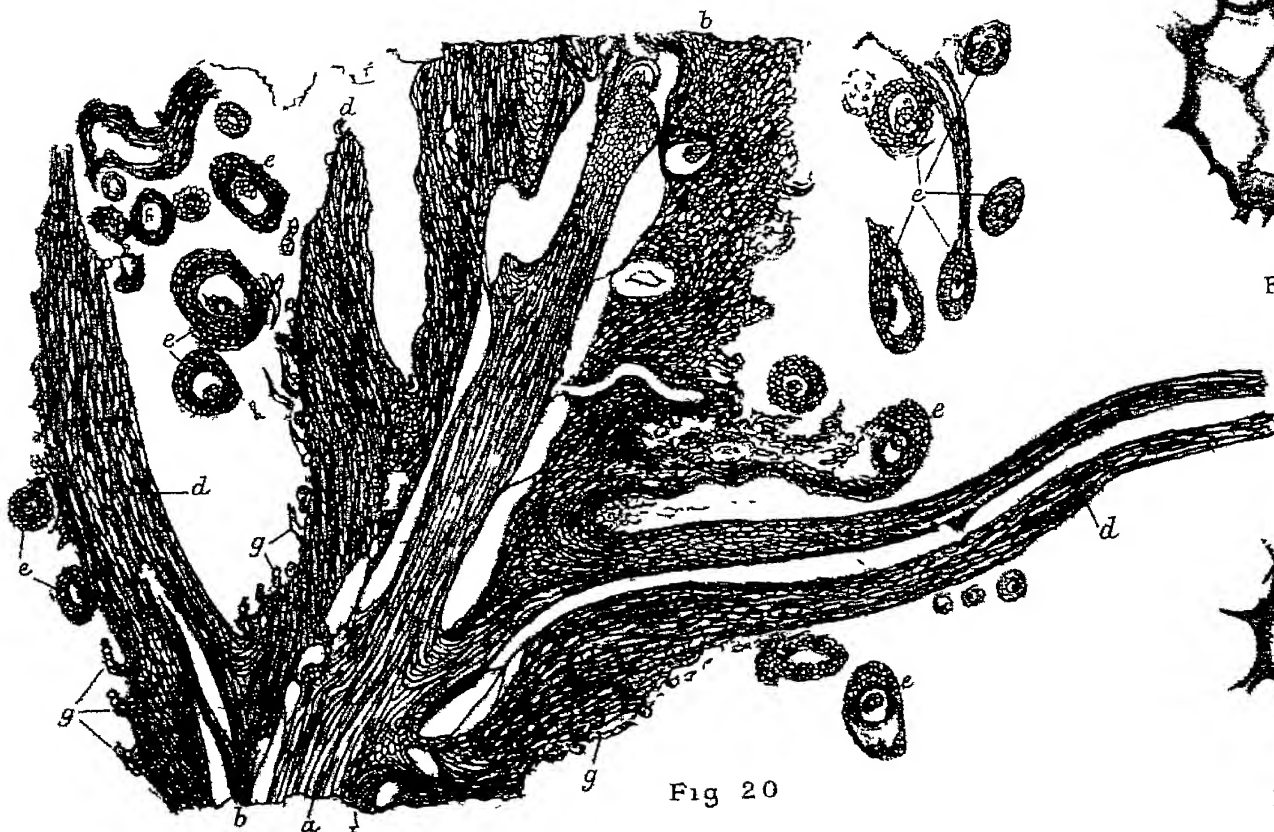








Fig 9

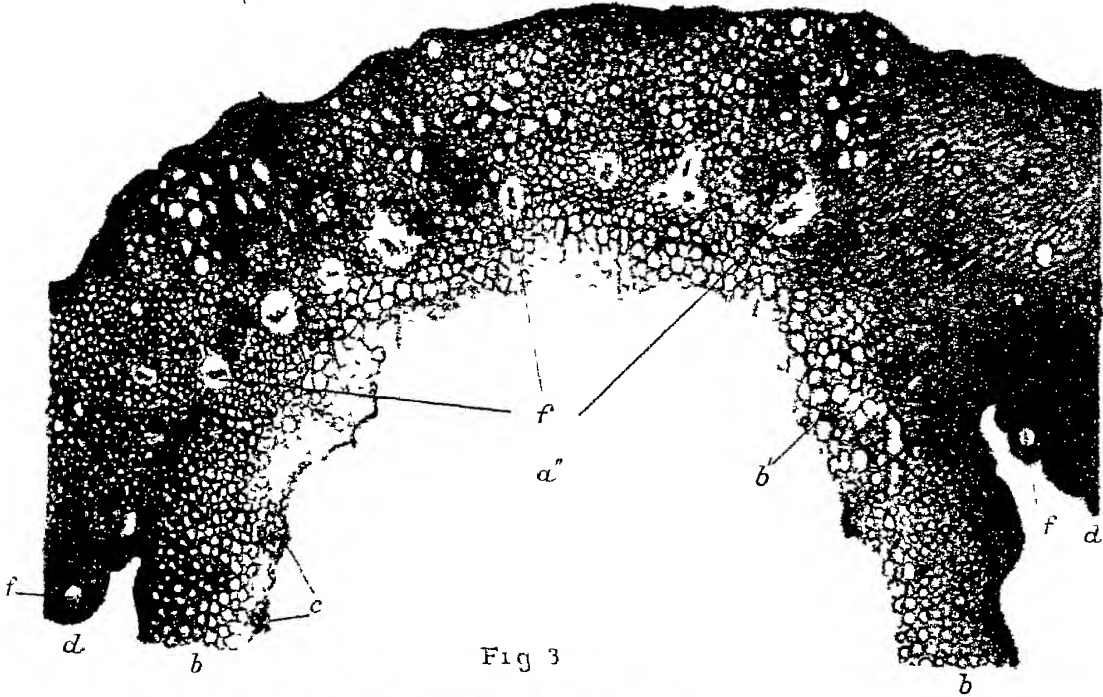


Fig 12

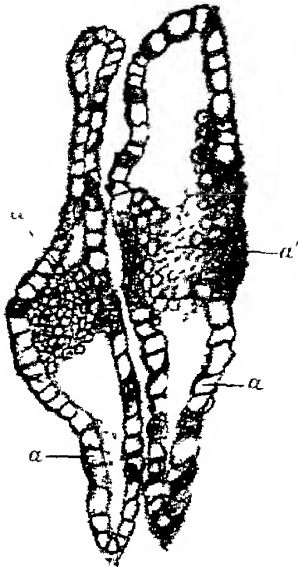


Fig 3

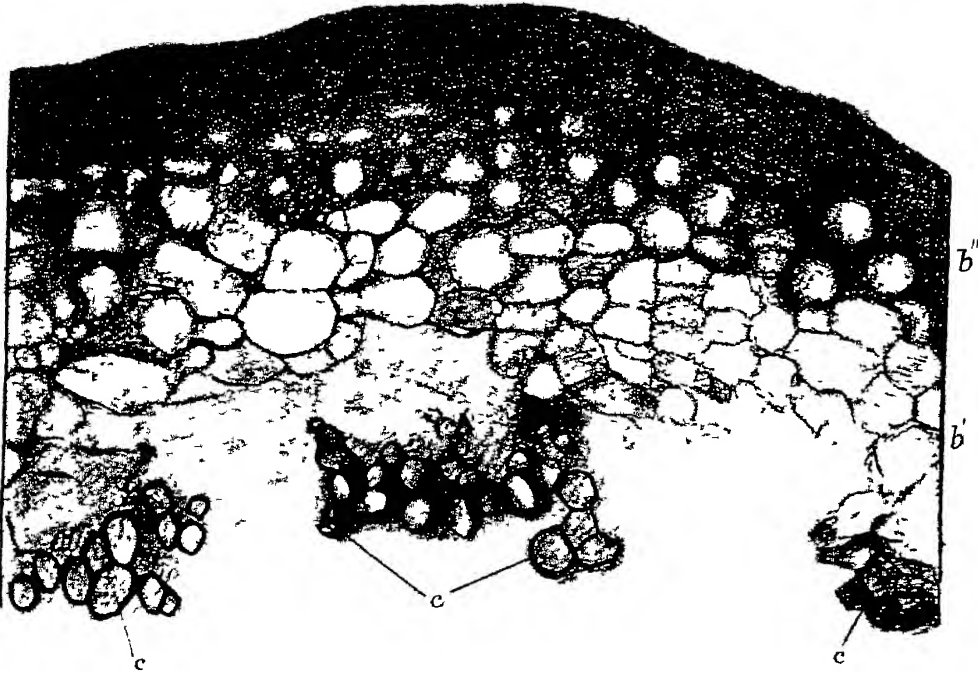


Fig 16

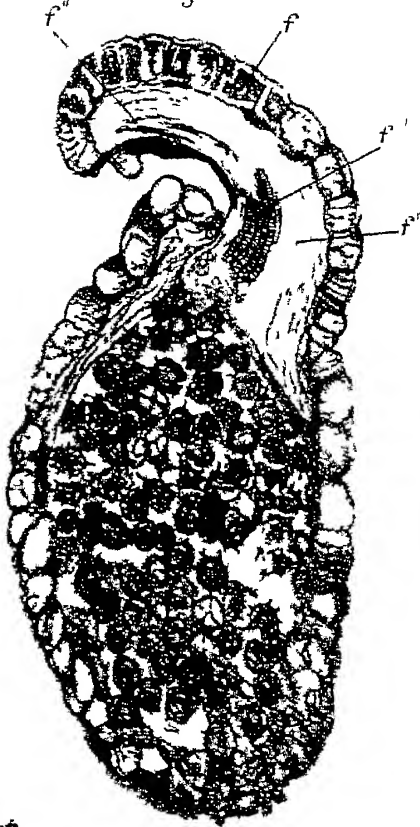


Fig 28

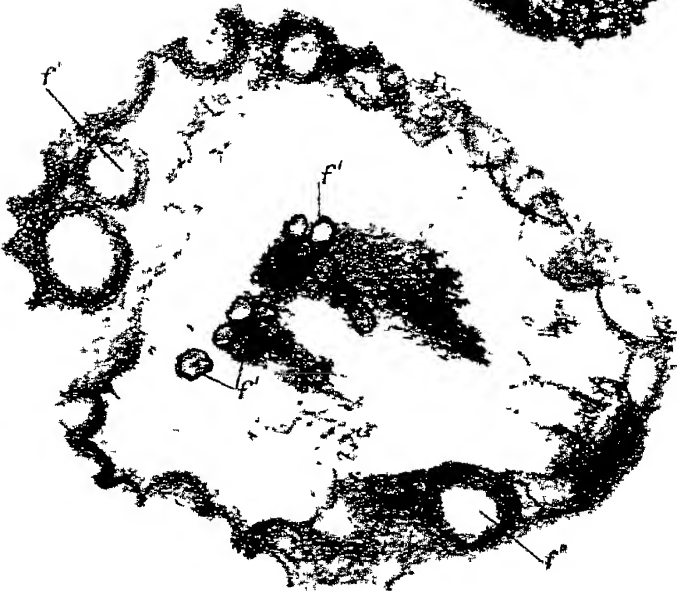
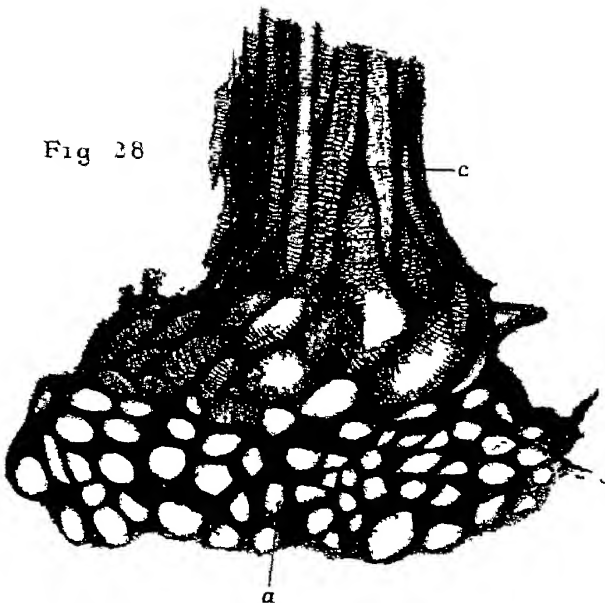


Fig 13





Fig 6

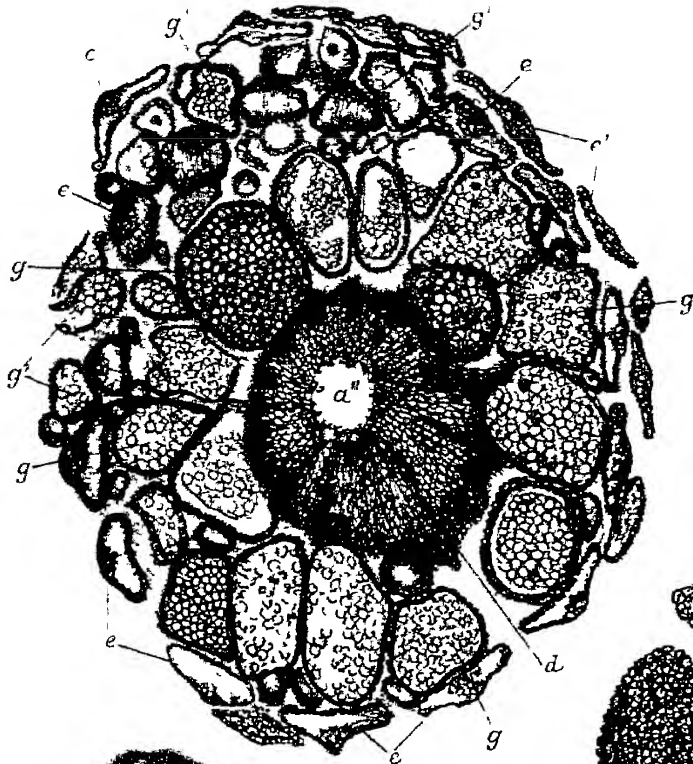


Fig 21

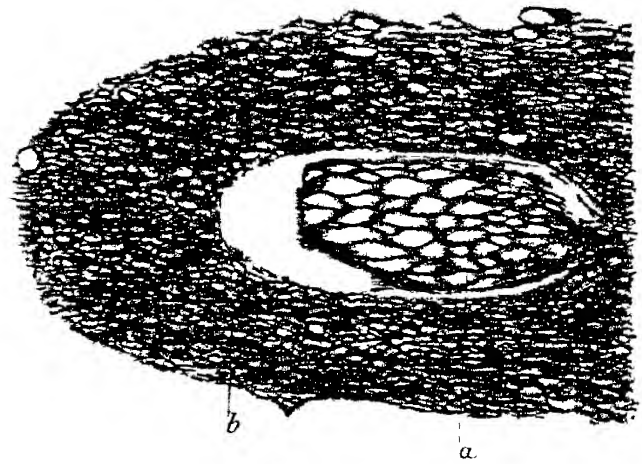


Fig 23

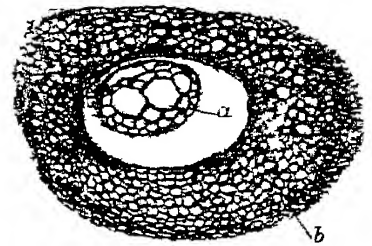


Fig 22

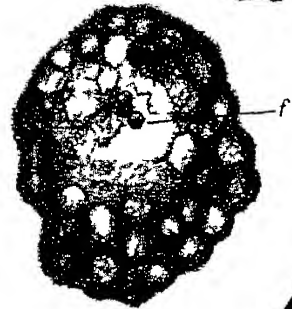
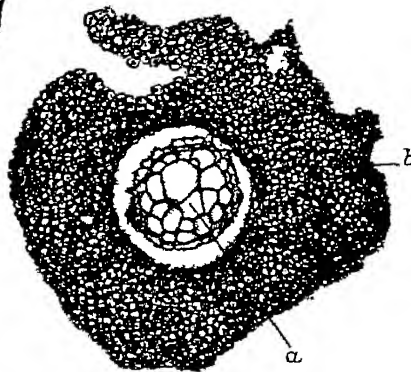


Fig 15

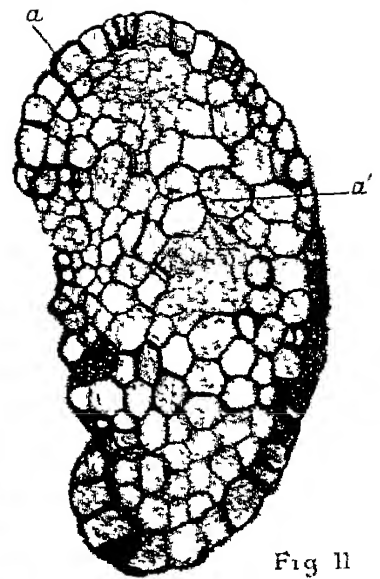


Fig 11

Fig 19

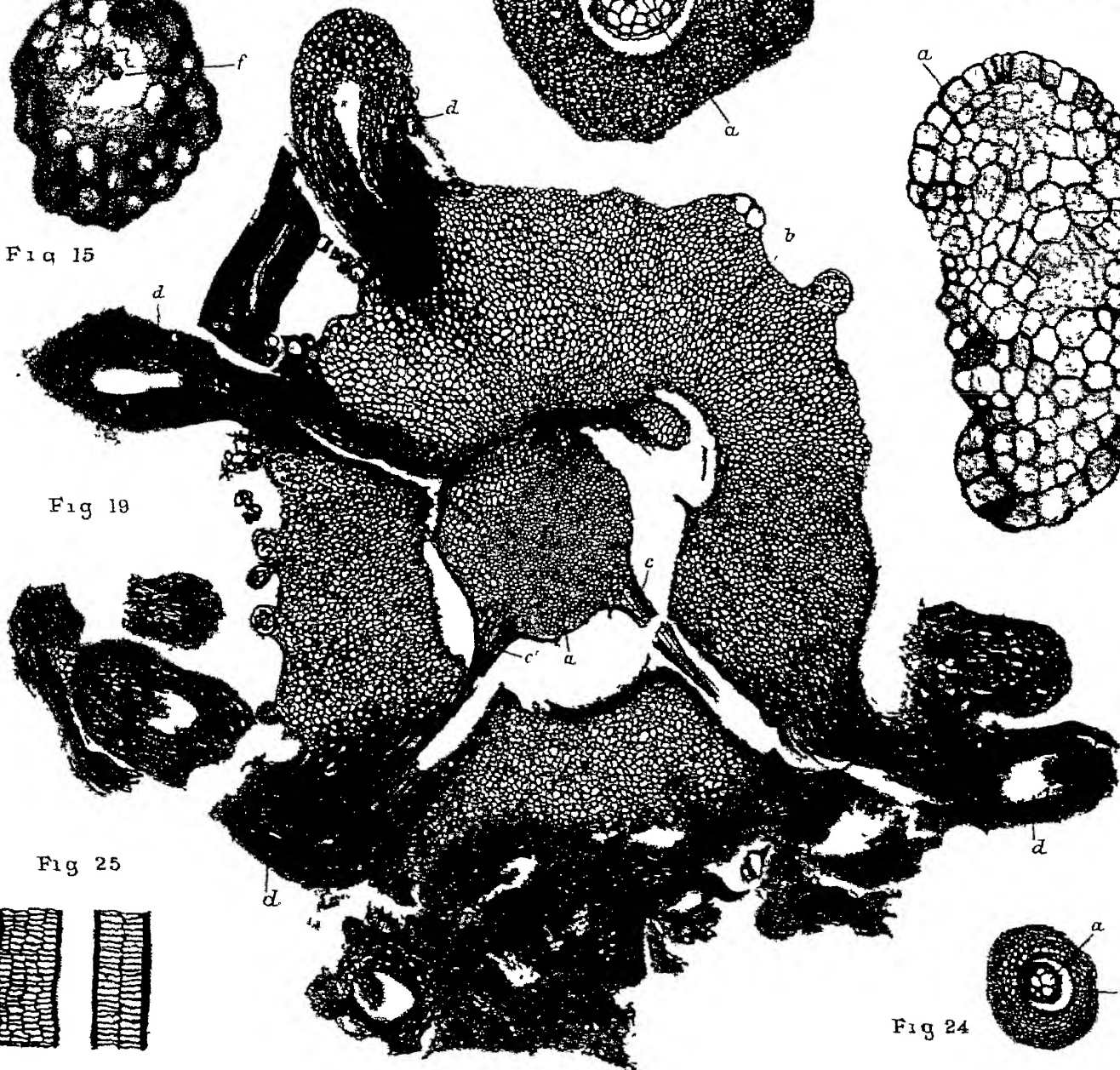
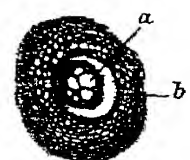


Fig 25



Fig 24









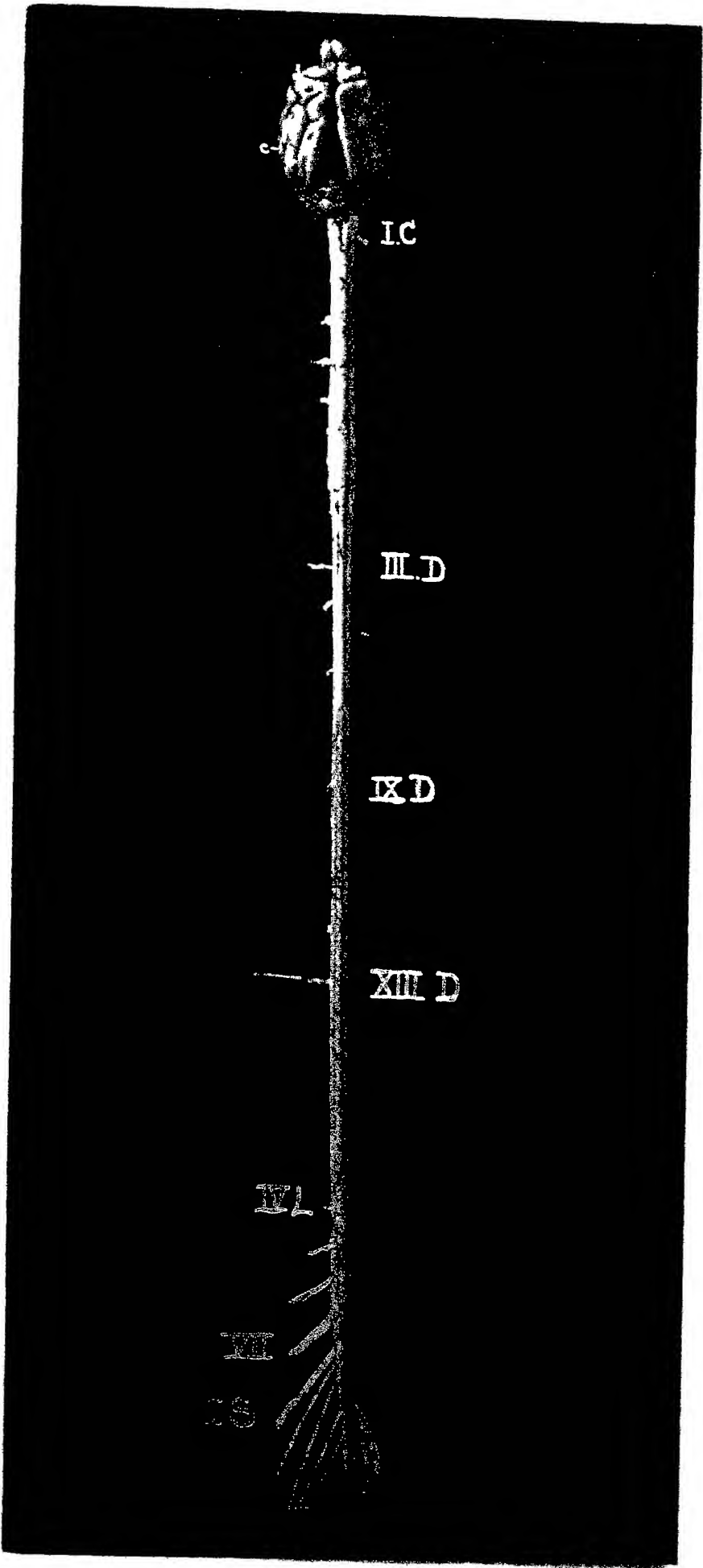


Photo-Print

L.B. Fleming Hamwell

VAT ADULT ♀



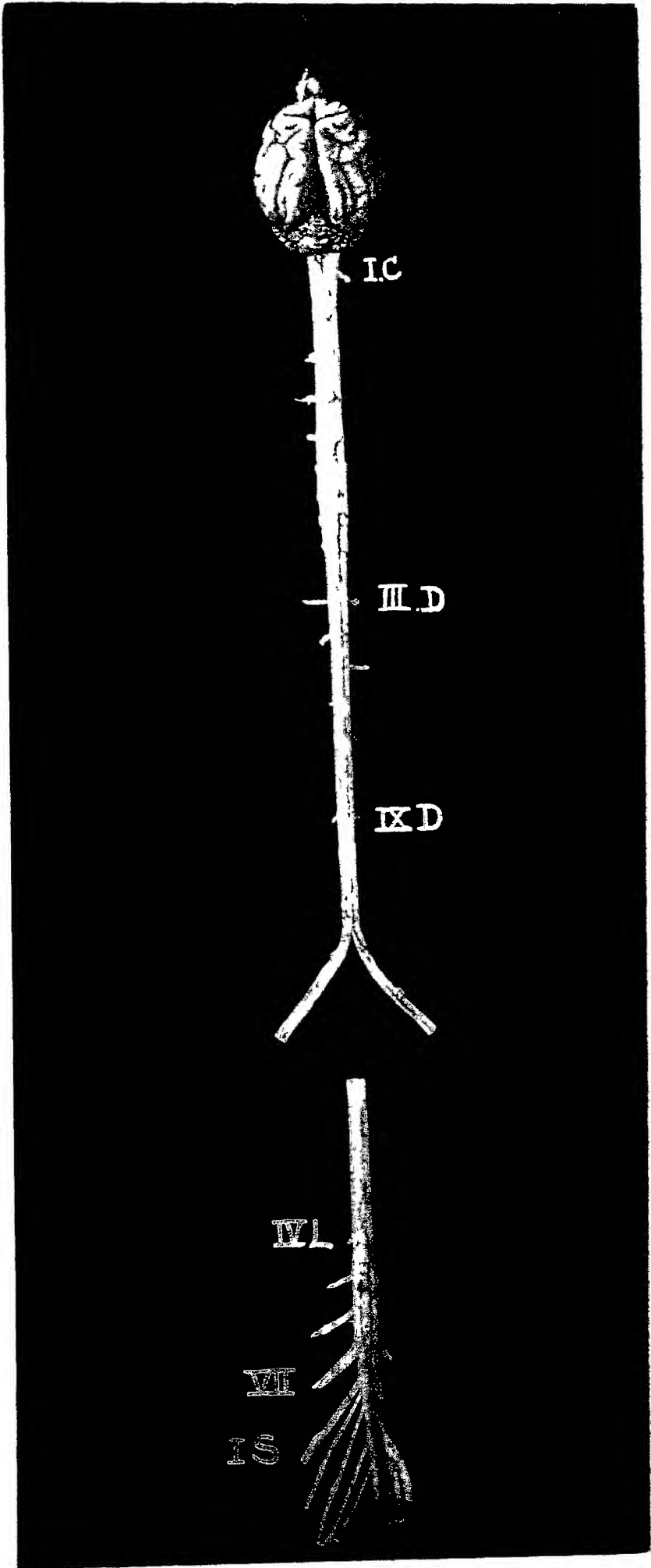


Photo-Print.

L.B. Fleming Hamwell

CAT ADULT 7





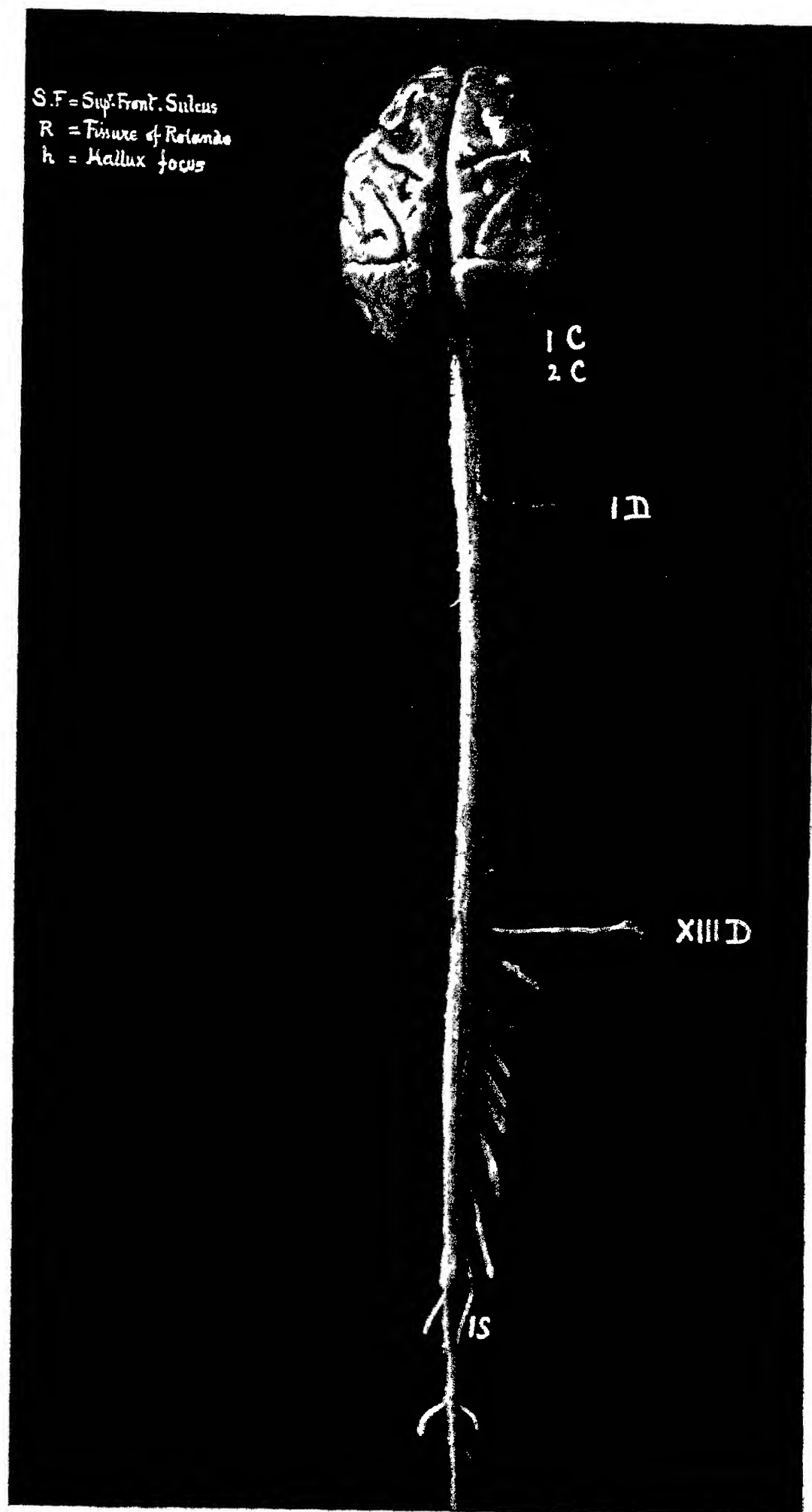


Photo-Print.

- B Fleming Maxwell

MACACUS PHEBUS ADULT ♀



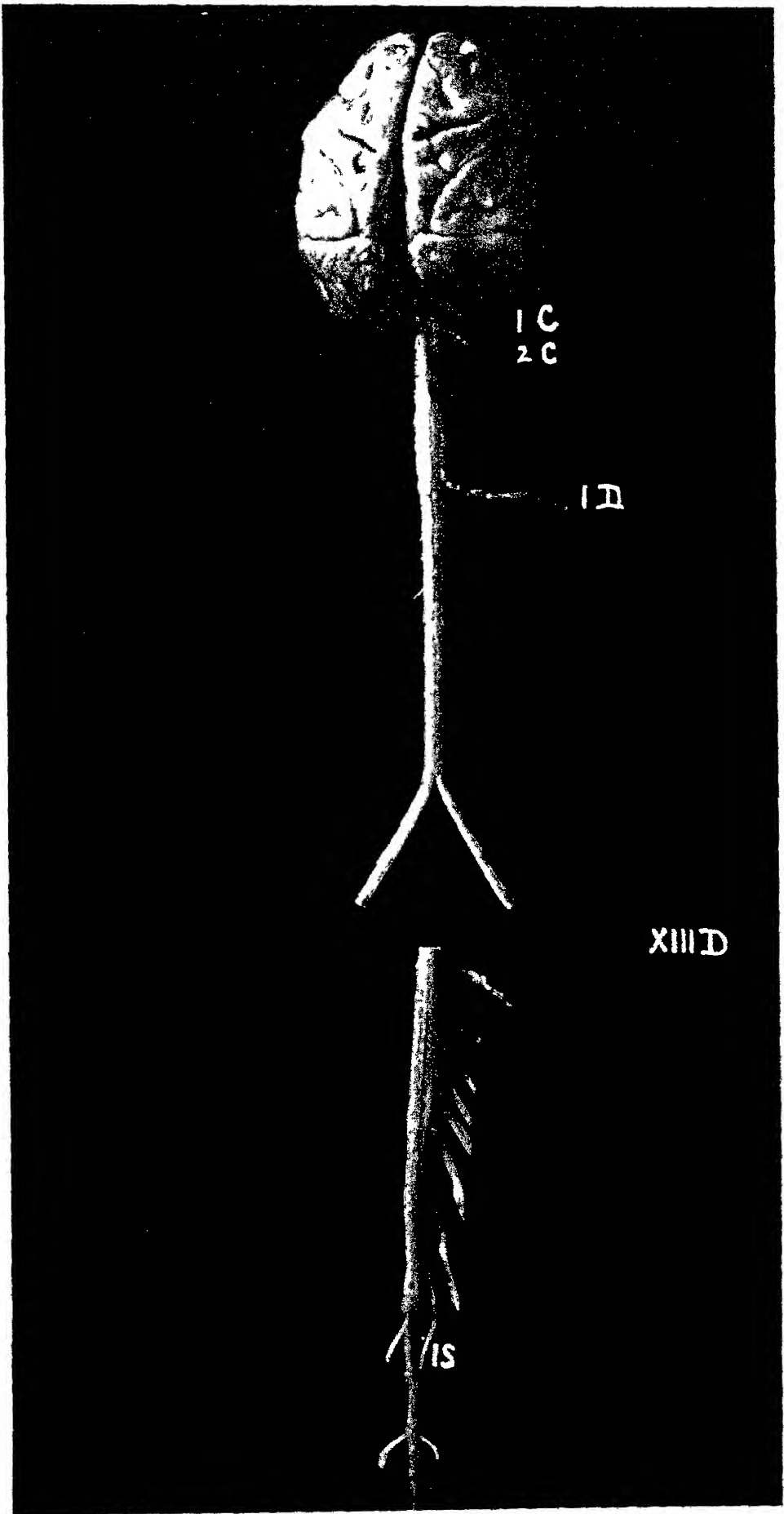
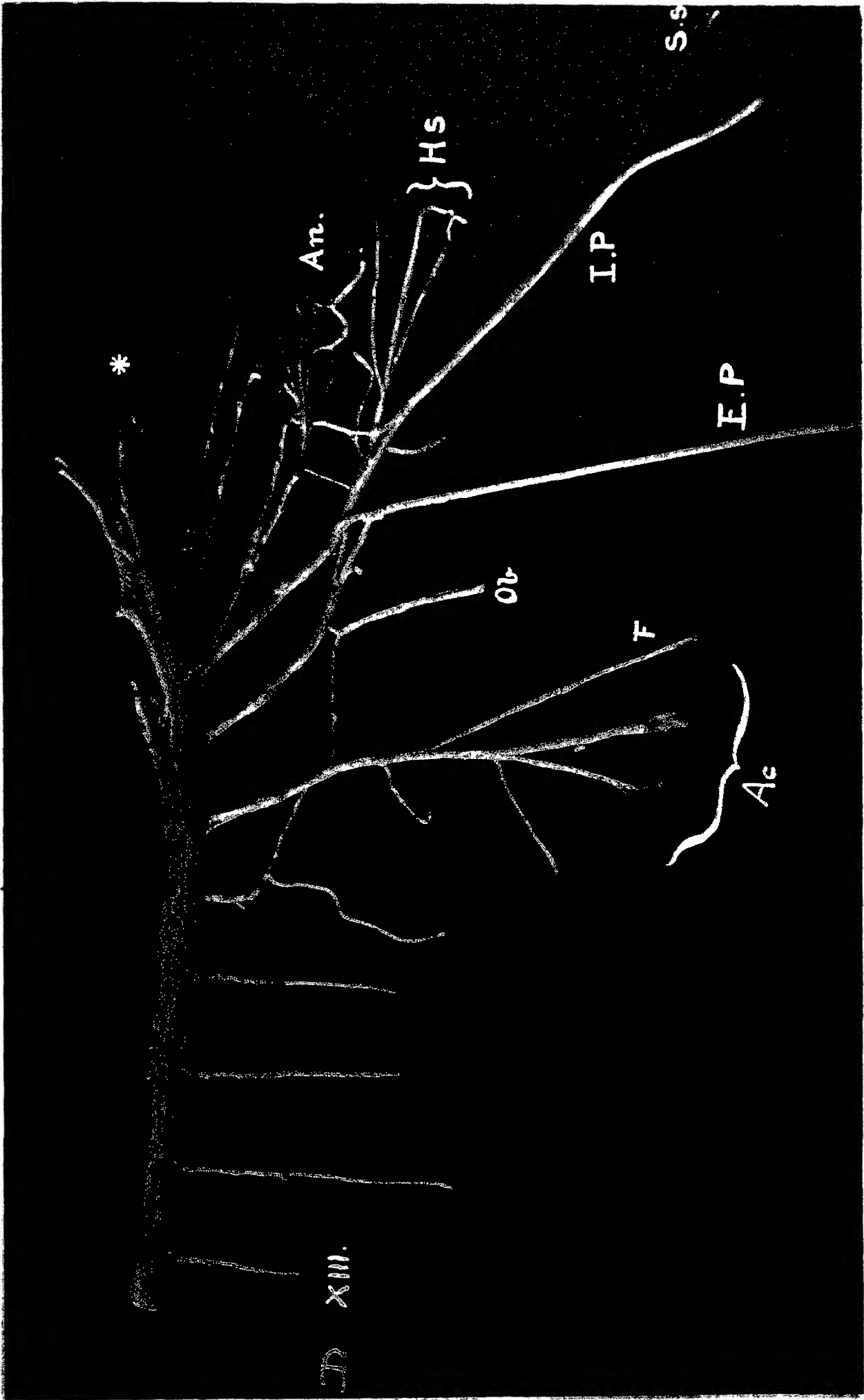


Photo-Print.

L.B. Fleming, Harvard

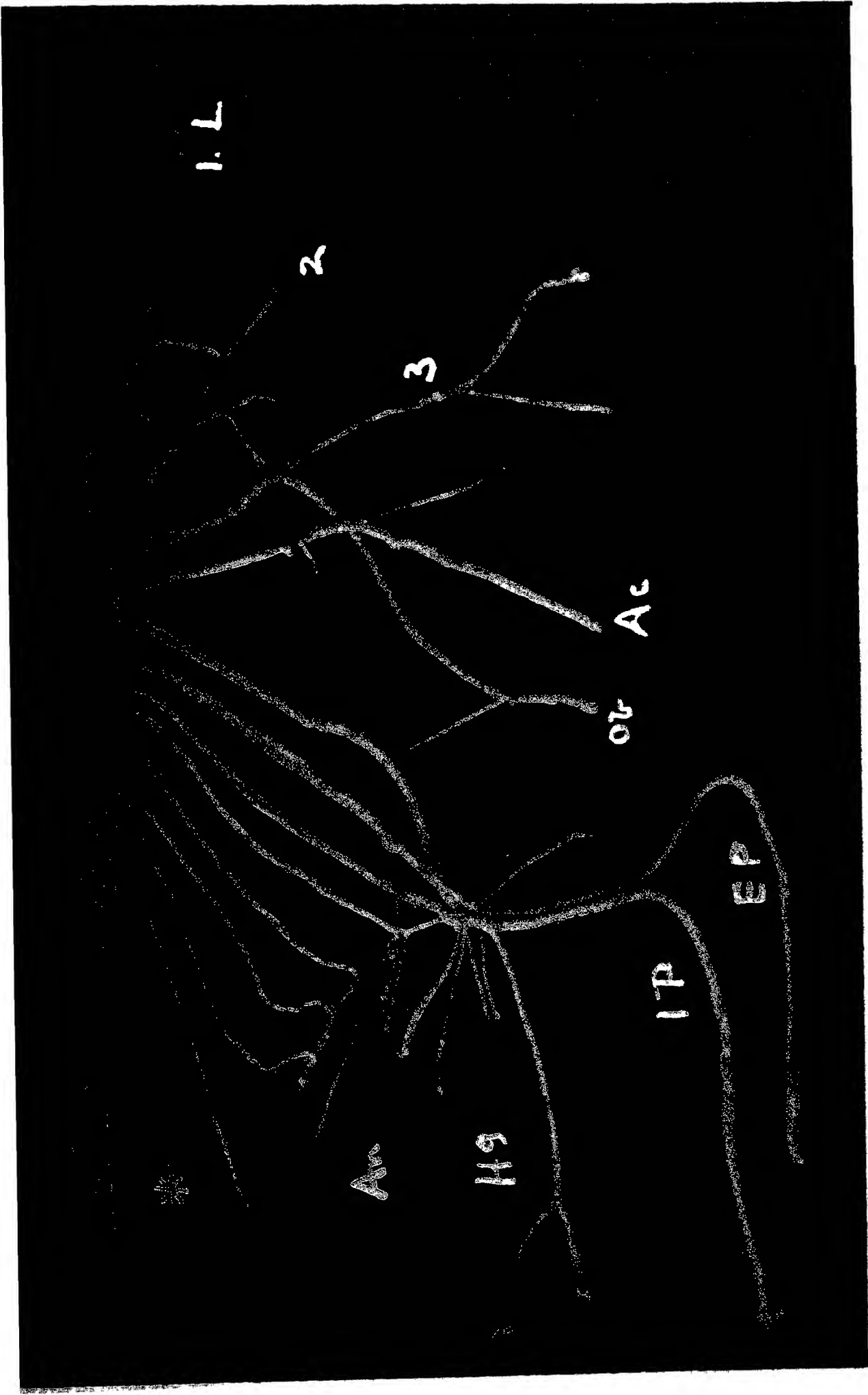
MACACUS RHESUS ADULT ♀





LUMBAR PLEXUS (CAT ADULT ♀)





Ac. Print

LUMBAR PLEXUS (MACCARTHY'S REVISION) PLATE 35











Fig 1

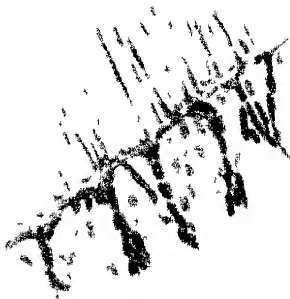


Fig 2

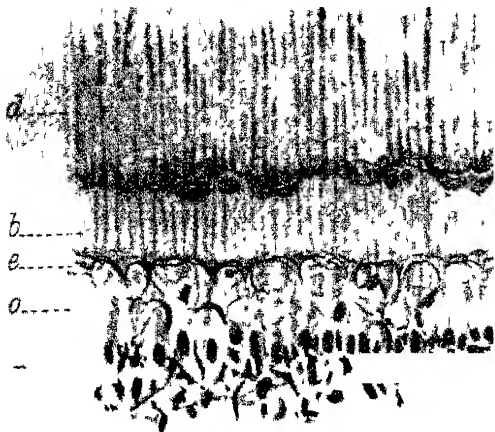
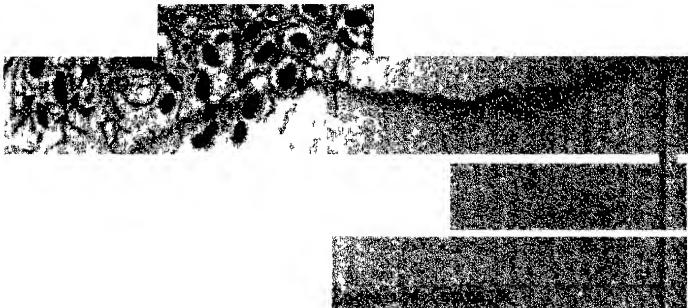
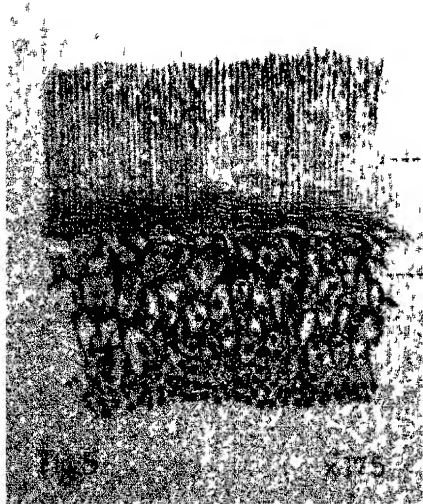


Fig 3



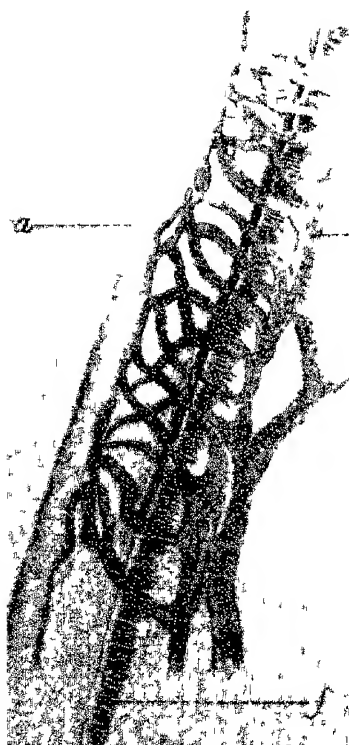
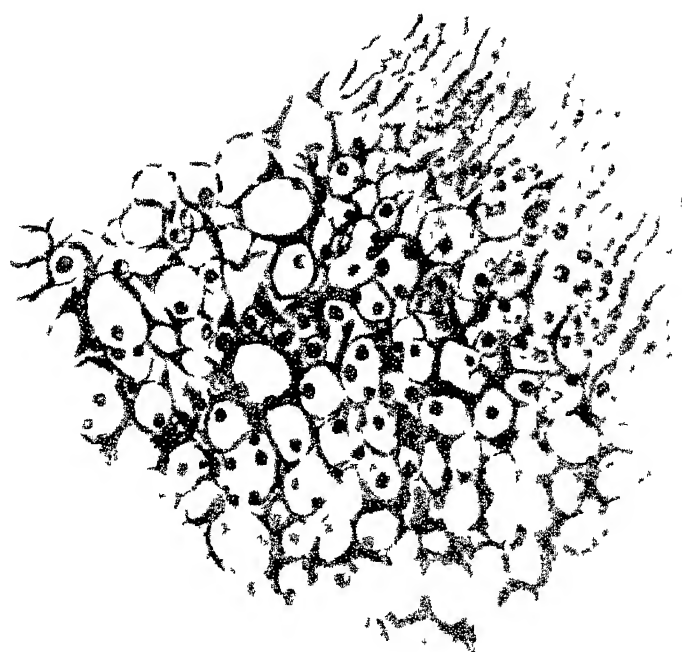
Fig 4







*Fig. 1.*











**Plate 40.**

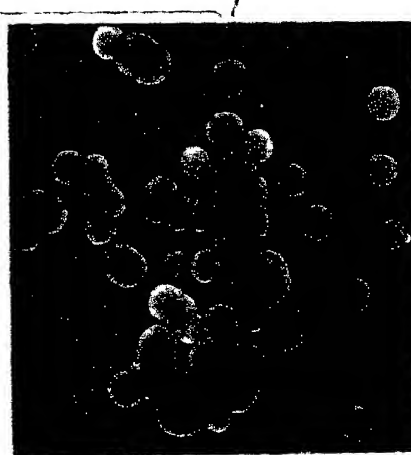
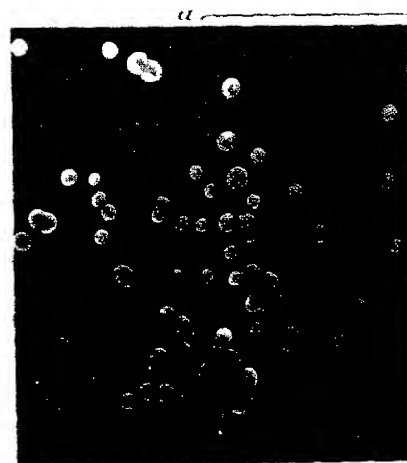
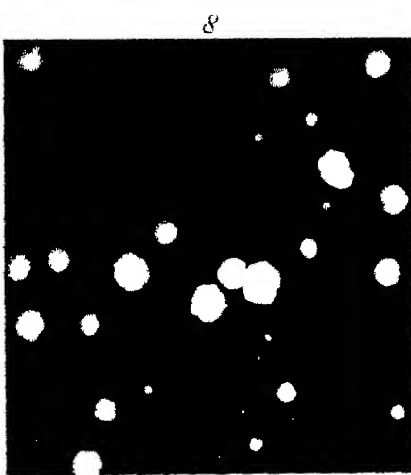
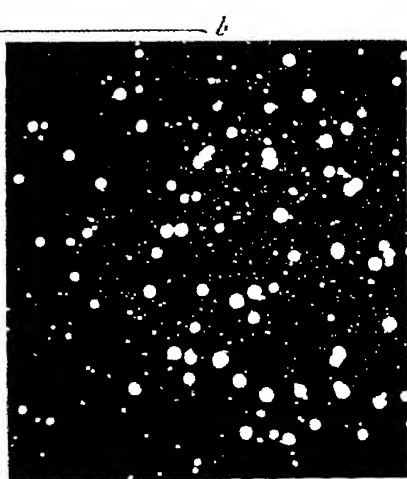
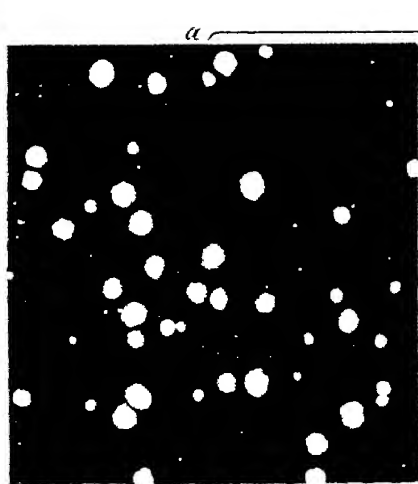
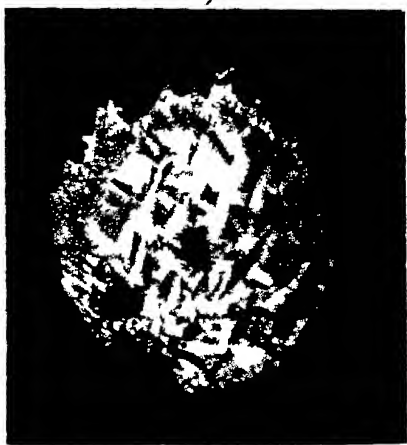
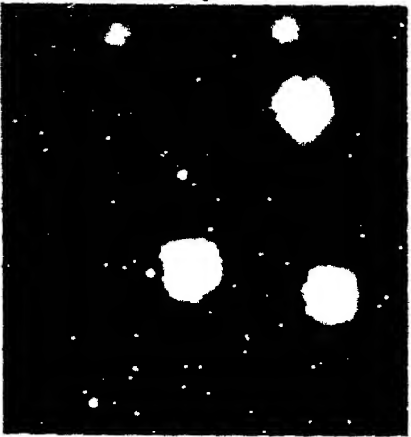
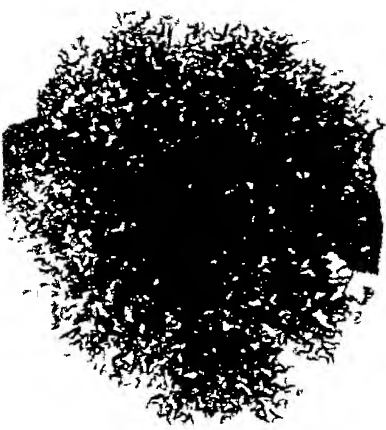
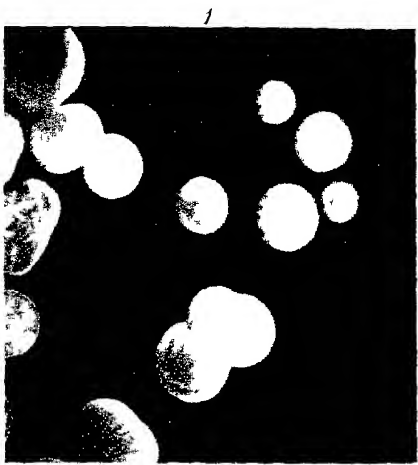
## PLATE 40.

PURE GELATINE PLATE CULTIVATIONS. TEMPERATURE OF INCUBATION, 20–23° C

These figures are mainly intended as a photographic record of the relative rapidity of growth of the several organisms, and the widely differing ages of the cultures should be noted when comparing the figures, *e.g.*, fig 6 is a plate culture five days old, whilst fig. 9 is but two days old

- Fig. 1. Anaërobic No. 2, turbid liquefied circles, 2 days old (actual size).
- Fig. 2. Anaërobic No. 3, dry colony on gelatine, 7 days old,  $\times 50$ .
- Fig. 3. Anaërobic No. 4, filmy opalescent expansions, 2 days old (actual size)
- Fig. 4. Anaërobic No. 6, non-liquefied circular colonies, 5 days old (actual size).
- Fig. 5. Anaërobic No. 5, C.G.I. dark ground illumination, 3 days old,  $\times 50$
- Fig. 6. Aërobic No. 5, wax drop colonies, 5 days old (actual size).
- Fig. 7A. Aërobic No. 1, non-liquefied colonies, 2 days old (actual size)
- Fig. 7B. Aërobic No. 1 $\alpha$ , non-liquefied colonies, 2 days old (actual size)
- Fig. 8. Aërobic No. 4, non-liquefied colonies, 2 days old (actual size)
- Fig. 9. Aërobic No. 3, liquefied colonies, 2 days old (actual size).
- Fig. 10A. Aërobic No. 2, liquefied colonies, 24 hours old (actual size).
- Fig. 10B. Aërobic No. 2, liquefied colonies, 27 hours old (actual size).

PURE PLATE CULTIVATIONS







## PLATE 41

### PURE GELATINE STREAK AND STAB CULTIVATIONS. TEMPERATURE OF INCUBATION, 20-23° C

These figures not only show the relative rapidity of growth, but also the characteristic manner of growth in gelatine

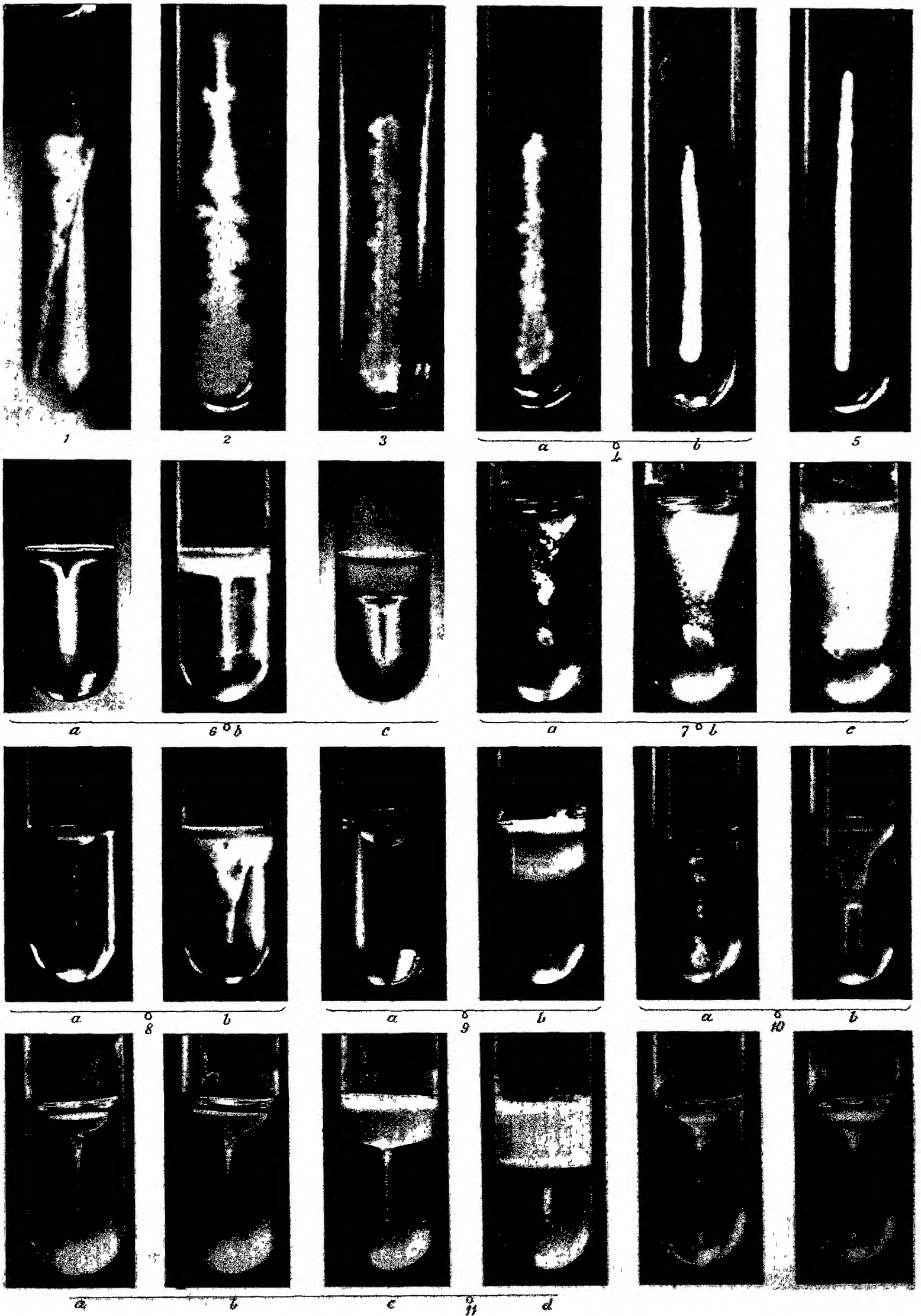
#### *Streak Cultures on Gelatine* (All actual size.)

- Fig. 1. Anaërobic No. 3, 7 days on gelatine and 7 days in broth.
- Fig. 2. Anaërobic No. 4, 2 days old
- Fig. 3. Aerobic No. 4, 3 days old.
- Fig. 4A. Aerobic No. 1, 3 days old.
- Fig. 4B. Aerobic No. 1 $\alpha$ , 3 days old.
- Fig. 5. Aerobic No. 5, 3 days old.

#### *Stab Cultures in Gelatine.* (All actual size.)

- Fig. 6A. Anaërobic No. 1, 24 hours old.
- Fig. 6B. Anaërobic No. 1, 48 hours old.
- Fig. 6C. Anaërobic No. 1, 5 days old.
- Fig. 7A. Anaërobic No. 2, 3 days old.
- Fig. 7B. Anaërobic No. 2, 5 days old.
- Fig. 7C. Anaërobic No. 2, 7 days old.
- Fig. 8A. Aerobic No. 3, 24 hours old.
- Fig. 8B. Aerobic No. 3, 2 days old.
- Fig. 9A. Aerobic No. 6, 7 days old.
- Fig. 9B. Aerobic No. 6, 14 days old.
- Fig. 10A. Anaërobic No. 2, 3 days old (old culture).
- Fig. 10B. Anaërobic No. 2, 3 days old (new culture)
- Fig. 11A. Aerobic No. 2, 24 hours old (new culture).
- Fig. 11B. Aerobic No. 2, 27½ hours old (new culture)
- Fig. 11C. Aerobic No. 2, 2 days old (new culture).
- Fig. 11D. Aerobic No. 2, 4 days old (new culture)
- Fig. 11E. Aerobic No. 2, 3 days old (old culture).
- Fig. 11F. Aerobic No. 2, 7 days old (old culture).

PURE STREAK & STAB CULTIVATIONS.







**Plate 42.**

## PLATE 42.

### PHOTO-MICROGRAPHS.

- |  |       |
|--|-------|
| Fig. 1. Anaërobic No. 1, cover-glass impression, gelatine plate 20 hours old,<br>edge of colony, long rods . . . . .                               | × 740 |
| Fig. 2. Anaërobic No. 1, cover-glass impression showing short rods and<br>swarmers . . . . .   | × 740 |
| Fig. 3. Anaërobic No. 1, surface growth on gelatine plate, 20 hours old<br>(from the stained plate direct). . . . .                                | × 100 |
| Fig. 4. Anaërobic No. 2, short rods . . . . .  | × 740 |
| Fig. 5. Anaërobic No. 2, involution forms . . . . .  | × 740 |
| Fig. 6. Anaërobic No. 5, cover-glass impression, colony 3 days old, single<br>layers of rods only fixed and stained, showing wave-like arrangement | × 370 |
| Fig. 7. Anaërobic No. 3, broth culture, 24 hours old . . . . .   | × 740 |
| Fig. 8. Anaërobic No. 3, edge of colony on gelatine plate, 7 days old, nitric<br>acid method . . . . .   | × 370 |

PHOTOMICROGRAPHS



x740

1



x740

2



x100

3



x740

4



x740

5



x370

6



x740

7



x370

8



**Plate 43.**

# PLATE 43.

- |   |        |
|---|--------|
| Fig. 1. Anaërobic, No. 4, cover-glass impression, edge of colony showing long rods . . . . .                | × 740  |
| Fig. 2. Anaërobic No. 4, same impression, centre of colony showing short rods and cocci . . . . .           | × 740  |
| Fig. 3. Aërobic No. 1α, encapsuled rods, pure colony from the surface of sewage direct . . . . .            | × 740  |
| Fig. 4. Aërobic No. 5, from colony on gelatine plate 4 days old, showing all the transition forms . . . . . | × 740  |
| Fig. 5. Aërobic No. 6, micrococci, from gelatine culture . . . . .  | × 740  |
| Fig. 6. Aërobic No. 4, cover-glass impression, edge of colony . . . . .                                     | × 740  |
| Fig. 7. Aërobic No. 3, cover-glass impression, surface of broth . . . . .                                   | × 740  |
| Fig. 8. Aërobic No. 3, enlargement showing group of spore bearing rods . . . . .                            | × 1500 |

